Small Mammal Taphonomy and Utilization by Middle Stone Age Humans in the Cape Floristic Region of South Africa

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DISSERTATION ABSTRACT

Though evidence for the creation and use of symbols and for technological and social complexity have emerged from the Cape Floristic Region of South Africa (CFR) that date to the Middle Stone Age (MSA), 285 – 30 thousand years ago, the relationship between these factors and the foraging strategies and use of landscapes by MSA humans remains anomalous, particularly in relation to small mammals (<4.5 kg adult body weight) and size 1 bovids (<20 kg adult body weight). This study is a taphonomic assessment which centers on the role of small mammals in the resource base of humans during the MSA and ─ together with large mammal, tortoise, and shellfish ─ provides a more complete understanding of the range of human subsistence strategies and foraging adaptations employed in the CFR during the MSA.

Data were collected and analyzed from two MSA CFR fossil bone assemblages, Die Kelders Cave 1 (DK1) and Pinnacle Point site 5-6 (PP5-6). This study includes the small mammal and size class 1 bovid archaeofaunas from DK1 and PP5-6 and provides detailed taphonomic analyses of their remains in order to evaluate the degree to which humans, raptors, and mammalian carnivores were involved in their accumulation at these sites. In addition to the archaeological collections, actualistic control assemblages of known human, raptor (diurnal and nocturnal), and mammalian carnivore accumulation were specifically created and analyzed for this project. These control assemblages broaden the scope of accessible small mammal assemblage by featuring diverse

prey mammals of different sizes and builds as well as a variety of typical small mammal predators.

Analyses of the DK1 and PP5-6 small mammal archaeofaunas include a detailed evaluation of human, raptor, and mammalian carnivore bone surface modification frequencies and bone breakage patterns. In addition, comprehensive comparisons with the control assemblages of known accumulation were conducted in order to better understand the degrees to which humans, raptors, or mammalian carnivores contributed to the small mammal faunas at DK1 and PP5-6.

DK1 humans maximized the environmental yield by exploiting low-quality resources as evidenced by numerous cut-marked and burned small mammal fossils. This strategy may have been employed in response to localized environmental conditions and to greater human population densities. The humans who occupied PP5-6 did not exploit small mammals and instead focused on higher-quality resources like shellfish and large ungulates. Humans and predators did not accumulate small mammals in any substantial way at PP5-6, suggesting that these taxa may have been less abundant near the site and/or that humans could afford to concentrate exclusively on high-quality resources, perhaps because of a higher-yield local environment. Results of this study suggest that an adaptive response by humans to the environmental conditions of MIS4 was to maximize the resource yield of local habitats to include lower-quality resources when necessary. The incorporation of these resources in the face of

changing environmental and population pressures is a subsistence adaptation that has not been documented in the previous glacial phase of MIS6 and may have played a crucial role in the population stability and expansion evidenced by the substantial number of sites in the Cape dating to MIS4.

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DISSERTATION INTRODUCTION

Over the last decade a wealth of paleoanthropological and genetic research has emerged that suggests both the modern human lineage and behavioral repertoire first appeared in Africa during the Middle Stone Age (MSA), a period which began ca. 280,000 years ago (Tryon and McBrearty, 2002; 2006) and persisted until ca. 30,000 years ago (Deacon and Deacon, 1999; McBrearty and Tryon, 2005; Tryon and McBrearty, 2006). In South Africa, numerous archaeological sites dating to the last half of the MSA have produced evidence of behavioral characteristics thought to be central to the expansion of modern humans out of Africa. These behavioral attributes include: (1) the creation and use of symbols (d'Errico et al, 2005; 2008; Henshilwood, 2007; Henshilwood and Dubreuil, 2011; Henshilwood et al, 2009; 2011; Mackay and Welz, 2008; Texier et al, 2010; Watts, 2010), (2) technological and social complexity (Brown et al, 2009; 2012; Conard and Will, 2015; d'Errico et al, 2007; 2012; Henshilwood et al, 2001b; Jacobs et al, 2008b; McCall and Thomas, 2012; Porraz et al, 2013; Wadley and Jacobs, 2006; Wadley et al, 2011; Wilkins et al, 2012), and (3) adaptable foraging strategies and use of landscapes (Clark and Kandel, 2013; Deacon, 2001; Dusseldorp, 2010; 2012; 2014; Faith, 2008; Jerardino and Marean, 2010; Karkanas et al, 2015; Marean, 2014; Marean et al, 2007; 2014; Nash et al, 2014; Steele and Klein, 2009; Thompson, 2010a; Wadley, 2010).

As a result of these research advancements, our understanding of the lifeways of MSA humans in Africa has greatly improved. There is little doubt that MSA humans were proficient hunters that preyed upon a variety of large ungulates (Faith, 2013; Marean et al, 2000a; Milo, 1998; Thompson, 2010b; Thompson and Henshilwood, 2011), including some of the most dangerous prey animals (Faith, 2008; 2011). It is also evident that MSA humans exploited a range of non-ungulate protein resources that included patchy and less-mobile or sessile organisms such as shellfish (Avery et al, 2008; Jerardino et al, 2014; Jerardino and Marean, 2010; Klein et al, 2004; Langejans et al, 2012; Marean, 2014; Marean et al, 2007; Parkington, 2003; Steele and Klein, 2005/6; 2008) and tortoises (Avery et al, 2008; Henshilwood et al, 2001a; Klein et al, 2004; Klein and Cruz-Uribe, 1983; 2000; Steele and Klein, 2005/6; 2013; Thompson, 2010b; Thompson and Henshilwood, 2014a; 2014b).

However, despite the fact that portions of South Africa currently and historically have supported a wide variety of small-bodied mammals (mole-rats, leporids, porcupine, rock hyrax, small carnivores, and others) and small-bodied ungulates (klipspringer, steenbok, and grysbok), many of which occur in large abundance at MSA archaeological sites, the role of smaller mammals (those between 4.5 kg and .75 kg adult body weight, e.g. animals the size of a house cat or cotton tail rabbit) in the resource base of MSA humans has not received a level of scrutiny comparable to that of large mammal archaeofaunas or shellfish. For instance, the small mammal component of the mammalian archaeofaunas at

a few prominent South African MSA sites account for approximately 93%, 85%, 50%, and 35% by NISP of all mammals at Ysterfontein 1 (Avery et al, 2008), Die Kelders Cave 1 (Klein and Cruz-Uribe, 2000), Blombos Cave (Henshilwood et al, 2001a), and Diepkloof Rockshelter (Steele and Klein, 2013), respectively.

Analyses which include small mammals can provide a more complete understanding of MSA diet – in particular subsistence strategies and foraging adaptations – as there is abundant ethnographic and ethnoarchaeological (Bird et al, 2005; 2009; Hill and Hawkes, 1983; Hill et al, 1987; Lee, 1979; Lupo and Schmitt, 2002; Noss and Hewlett, 2001; Yellen, 1977; 1991a; 1991b) evidence as well archaeological (Broughton, 1994a; 1994b; 1997; 1999; Butler and Campbell, 2004; Cannon, 2000; Hockett and Bicho, 2000; Hockett and Haws, 2002; McClure, 2004; Nagaoka, 2002; Stiner et al, 1999; 2000; Wadley, 1998) support from regions beyond South Africa to demonstrate that small mammals can account for a considerable portion of the forager diet.

For many forager populations small vertebrates constitute a sizable portion of the protein resource base. Yellen (1977; 1991ab) reported that over a multi-month study period 55% of the total prey mass taken by the !Kung were small mammals. Among the Ache, Hill and Hawks (1983) reported that 75% of acquired prey were small animals. In addition to the prey size composition, there often appears to be a sexual division of labor in relation to small game procurement. In some forager societies, small animals procured by women account for a substantial portion of the prey taken as well as a consistent supply

of nutritional protein (Bird and Bliege Bird, 2005; Bird et al, 2004; Bliege Bird and Bird, 2008; Lupo and Schmitt, 2002; Wadley, 1998).

For example, in their study of hunting techniques and sexual division of labor among the Bofi foragers of the Congo Basin, Lupo and Schmitt (2002) report that 145 of the 148 prey captured were small mammals or size 1 bovids, only three animals were medium-sized (>20 kg), and large prey (>100 kg) were not pursued at all during the time of the study. In another study, Bird et al, (2004; 2005) note that a variety of small vertebrates account for the bulk of foraging calories among the Martu of Australia's Western Desert and that women commonly acquire these prey; three different sand monitor species account for 35% of their foraging calories alone. Bird et al (2005) also report that hunters who pursued small game failed to capture prey only 3% of the time as compared to a 68% failure rate when pursuing larger prey species. Studies such as these demonstrate both the important contribution of women in protein procurement and the steady contribution of small prey towards the protein component of forager diet.

Research which includes small mammals is therefore vital to the study of MSA lifeways. This study is a detailed taphonomic assessment of MSA small mammal accumulations designed to address the research disparity between small and large prey through the assessment of small mammals and size class 1 bovids (antelopes <20 kg adult body weight, roughly the size of a border collie;

Brain, 1974) from Die Kelders Cave 1 (DK1) and Pinnacle Point Site 5-6 (PP5-6), each located in the Cape Floristic Region of South Africa, and principally occupied during marine isotope stages 4 and 5a-c (MIS4, MIS5; 71 – 57,000 and 96 – 71,000 respectively). Also included in this analysis for comparison with the MSA archaeofaunas is the Later Stone Age (LSA) component of DK1, an assemblage that was undoubtedly accumulated by fully modern humans.

The aim of this study is to provide taphonomic analyses of the DK1 and PP5-6 faunas in order to evaluate the degree to which humans, raptors, and mammalian carnivores were involved in the accumulation of small mammals and size 1 bovids at these sites. Included is a detailed evaluation of human, raptor, and mammalian carnivore bone surface modification frequencies, bone breakage patterns, and skeletal-part representation as means to differentiate between the relative contributions of different predators.

This study also includes taphonomic comparisons of the DK1 and PP5-6 small mammals with both naturally- occurring and experimentally-created control assemblages of known human, raptor (diurnal and nocturnal), and mammalian carnivore accumulation. These assemblages were created and analyzed specifically for this project (with the exception of the Dobe Base Camp collection). The control assemblages include: !Kung San produced Dobe Base Camp ethnoarchaeological remains (Yellen, 1991ab; Armstrong, paper in preparation), modern South African Verreaux's eagle prey accumulations

(Armstrong and Avery, 2014), and experimentally produced bald eagle, great horned owl, and coyote prey assemblages (Armstrong, 2015).

To address the question of accumulation and small mammal utilization by humans during the South African MSA, as well as to expand the range and depth of taphonomic studies regarding this prey category, these major questions and disparities are addressed:

- Are the small mammal skeletal remains from the MSA and LSA deposits at DK1 and PP5-6 the refuse of past human inhabitants or other potential bone accumulators such as carnivores and raptors? There are three primary hypotheses: (1) the remains were predominantly accumulated by raptors and carnivores, (2) the remains are predominantly due to humans, and (3) the remains are the result of combined human and non-human agency. To this end, a taphonomic and zooarchaeological assessment of the small mammals from DK1 and PP5-6 has been conducted in order to identify accumulator patterning.
- What were the subsistence practices and strategies of MSA humans as evidenced by the DK1 and PP5-6 assemblages? There are three primary hypotheses: (1) that MSA humans did not regularly exploit lower-ranked prey, that (2) high-ranked, large prey were preferentially exploited over smaller mammals, and that (3) protein procurement strategies were consistent between the two sites over time. To test these hypotheses, an assessment of species diversity, relative abundance indices, and bone surface modification analyses

have been conducted utilizing the small mammal data collected for this project as well as previously published data regarding DK1 and PP5-6 and other CFR MSA sites.

- Is it possible to distinguish between small mammals accumulated by humans, raptors (diurnal and nocturnal), and mammalian carnivores? The study of small mammal taphonomy has lagged behind that of larger mammals and micro-mammals. With some exceptions (Elkin and Mondini, 2001; Erlandson et al., 2007; Hockett, 1999; Lant, 2007; Lloveras et al., 2008a; 2008b; 2009; 2010; 2012a; 2012b; Lupo and Schmitt, 2002; 2005; Mondini, 2004; Schmitt and Lupo, 2008; Tagliacozzo and Fiore, 1998; Yellen, 1991a; 1991b, and others), small mammal taphonomy has tended to focus on skeletal-part profile analysis of leporids at the expense of both bone surface modification analysis and a representative range of small mammal prey taxa that commonly occur at archaeological sites. Analyses that include bone surface modifications in addition to skeletal-part profiles and address a range of prey taxa of different size and build will provide a stronger means for identification of fossil bone accumulators.

The body of small mammal taphonomic research regarding surface modifications and prey taxa diversity is considerably expanded through the analysis of: (1) the Dobe Base Camps ethnoarchaeological assemblage of know human origin which features hare, size 1 bovid, porcupine, and springhare remains; (2) the medium carnivore (*Canis latrans*), diurnal raptor (*Haliaeetus*

leucocephalus), and nocturnal raptor (*Bubo virginianus*) experimental feeding assemblages, each featuring rabbits and guinea pigs, small prey of differing size and body proportion (furthermore, guinea pigs are similar in size and build to the Cape dune mole-rat which makes up the bulk of small mammals at DK1); and (3) naturally-accumulated southern African diurnal raptor prey remains (*Aquila verreauxii*) consisting of Cape dune mole-rats, rock hyraxes, size 1 bovids, and small carnivores. Humans, mammalian carnivores, and nocturnal and diurnal raptors are the hypothesized accumulators of small prey at PP5-6 and DK1 (Avery, 2000; Cruz-Uribe and Klein, 1998; Klein and Cruz-Uribe, 2000; Marean et at, 2000). The taphonomic assessment of small mammal assemblages of known accumulation provides empirical support toward the identification of the accumulator(s) these sites.

Dissertation structure: This dissertation follows a three paper format where the intent is for each paper to be submitted to a peer-reviewed journal. These papers are separate chapters of this dissertation. In addition to the three papers, this dissertation consists of an introduction and concluding chapters as well as abridging chapters linking the papers.

Paper 1, co-authored with Graham Avery from the Natural History Collections Department, Iziko South African Museum in Cape Town, is titled "Taphonomy of Verreaux's Eagle (*Aquila verreauxii)* prey accumulations from the Cape Floral Region, South Africa: implications for archaeological interpretations."

The paper was published in the *Journal of Archaeological Science,* volume 52, 2014. We conducted a taphonomic analysis of modern prey accumulations of Verreaux's eagle from the Cape Floristic Region. Verreaux's eagles nest in or around cliffs and rocky outcrops, places that also attract other bone accumulators, including humans. Therefore, it is necessary to characterize the signatures of Verreaux's eagle bone accumulation with as much precision as possible in order to differentiate between the prey remains of other bone accumulators, especially in relation to fossil assemblages that originate in and around cliffs, rock shelters, and caves. Towards this end, we describe the taxonomic composition, skeletal-part representation, bone breakage patterns, and bone surface modifications of mammal bones as well as the range of variability within those signatures.

Based on the frequency of bone modifications we determined that Verreaux's eagle modify the bones of their prey more often than other eagle species. We suggest that taphonomic patterns derived from predation by other eagle taxa are not the most appropriate means to identify Verreaux's eagle predation in faunal assemblages. In addition, we conclude that there is patterned variability in the ways that Verreaux's eagle accumulate and modify the bones of their prey. There are two distinct skeletal-parts preservation, bone breakage, and bone surface modification patterns among the prey in our sample: one that characterizes rock hyraxes, mole-rats, and carnivores; and another that characterizes hares and small bovids. Faunal analysts investigating the potential

role of Verreaux's eagle at fossil sites should be aware of 1) these taphonomic patterns and differences and 2) that there is no singular pattern of accumulation among the eagle's prey. We define patterns of preservation, breakage, and bone modification that can be employed on a taxon-specific basis to distinguish Verreaux's eagle prey remains from other bone accumulators, including humans.

Paper 2 is titled "Eagles, Owls, and Coyotes (Oh My!): Taphonomic analysis of rabbits and guinea pigs fed to captive raptors and coyotes." This paper is accepted for publication in the *Journal of Archaeological Science: Reports* but at the time of writing this has not yet been published. The aim of this paper is to address the potential for multiple accumulating agents of small mammals at fossil sites. However, the lack of diverse predator and prey experimental and actualistic studies often makes it difficult to attribute the accumulator(s) of small mammals. I report the results of experimentally created assemblages of rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) fed to a bald eagle (*Haliaeetus leucocephalus*), great horned owl (*Bubo virginianus*), and coyote (*Canis latrans*). The analysis provides a taphonomic assessment of two small mammal taxa that differ in size and build and are broadly representative of small mammals recovered from archaeological sites. The ingested and non-ingested portions of the prey remains were analyzed for skeletal-part, digested-part, deleted-part, and fractured-part bone representation, bone breakage, and bone surface modifications. The rabbit and

guinea pig samples were compared and taphonomic differences between predators and prey taxa were observed.

The predators produced variable and distinctive intra- and interspecific skeletal-, digested-, deleted-, and fractured-part profiles. Bone surface modification frequency differences between the samples show a mixture of significant and non-significant intra- and interspecific comparisons. This study expands the range of small mammal experimental and actualistic studies to include prey of underrepresented size and build (guinea pigs) and characterizes the bone surface modifications of predator-accumulated small mammals. Archaeological assemblages often feature a mixture of accumulators (humans, raptors, and mammalian carnivores); this analysis of raptor and mammalian carnivore predation on rabbits and guinea pigs will aid in the differentiation of predation between these predators in archaeological contexts.

Paper 3 is titled “Small mammal utilization by Middle Stone Age Humans at Die Kelders Cave 1 and Pinnacle Point Site 5-6, Western Cape Province, South Africa.” This paper has not yet been submitted to a journal for publication; the aim is to eventually submit this paper to the *Journal of Human Evolution*. The paper reports the results of the taphonomic analysis of the small mammals and size 1 bovids from DK1 and PP5-6. This study provides the first comprehensive taphonomic analysis of MSA small mammals with a focus on discerning the role of humans in their accumulation and the implications for human behavioral adaptations in a region that features prominently in the investigation of modern

human origins. Based on comparisons with control assemblages of known accumulation by humans, mammalian carnivores, and raptors (nocturnal and diurnal), it is evident that humans accumulated Cape dune mole-rats, hares, and size 1 bovids from throughout much of DK1. Nocturnal raptors also accumulated small mammals at DK1 and are the main accumulator in strata where anthropogenic input is minimal, a result consistent with previous zooarchaeological analysis at DK1. The patterning of cut-marked and burned Cape dune mole-rat remains at DK1 provides the first evidence in the MSA for the systematic utilization of small mammals for their skins and as a protein source.

Unlike DK1, small mammals and size 1 bovids constitute only a small portion of the PP5-6 mammals and they exhibit little evidence of human accumulation. Taphonomic indicators reveal that nocturnal and diurnal raptors accumulated most of the small mammals and size 1 bovids at PP5-6. The nominal presence of small mammals in the PP5-6 fauna is atypical of MSA sites in the CFR, where small mammal taxa are abundant and often constitute large portions of MSA archaeofaunas.

With the assumption that the MSA occupation at DK1 dates to MIS4, DK1 humans maximized the environmental yield by exploiting low-quality resources, a strategy possibly employed in response to localized environmental conditions and to greater human population densities. In comparison, the MIS4 humans at PP5-6 did not exploit small mammals and instead focused on higher-quality

resources like shellfish and large ungulates. Humans and predators did not accumulate small mammals in any substantial way at PP5-6, suggesting that these taxa may have been less abundant near the site and/or that humans could afford to concentrate exclusively on high-quality resources, perhaps because of a higher-yield local environment. Results of this study suggest that an adaptive response by humans to the environmental conditions of MIS4 was to maximize the resource yield of local habitats to include lower-quality resources when necessary. The incorporation of these resources in the face of changing environmental and population pressures is a subsistence adaptation that has not been documented in the previous glacial phase of MIS6 and may have played a crucial role in the population stability and expansion evidenced by the substantial number of sites in the Cape dating to MIS4.

This taphonomic study allows for the evaluation of the role of small mammals in the resource base of humans at DK1 and PP5-6 and ─ together with large mammal, tortoise, and shellfish ─ a more complete understanding of the range of human subsistence strategies and foraging adaptations employed in the CFR during the MSA. By determining the role humans played in the accumulation of small mammals at these MSA sites, new information regarding human foraging adaptations and landscape use during this critical time period in human evolution will be added to a growing and evolving body of research.

PAPER 1:

Taphonomy of Verreaux's Eagle (*Aquila verreauxii*) prey accumulations from the Cape Floral Region, South Africa: implications for archaeological interpretations

SUMMARY

We conducted a taphonomic analysis of modern prey accumulations of Verreaux's eagle (VE; *Aquila verreauxii)* from the Cape Floral Region of South Africa. VE nest in or around cliffs and rocky outcrops, places that also attract other bone accumulators, including humans. Therefore, it is necessary to characterize the signatures of VE bone accumulation with as much precision as possible in order to differentiate between the prey remains of other bone accumulators, especially in relation to fossil assemblages that originate in and around cliffs, rock shelters, and caves. Towards this end, we describe the taxonomic composition, skeletal-part representation, bone breakage patterns, and bone surface modifications of mammal bones as well as the range of variability within those signatures. Based on the frequency of bone modifications we determine that VE modify the bones of their prey more often than do other eagle species. We suggest that taphonomic patterns derived from predation by other eagle taxa are not the most appropriate means to identify VE predation in faunal assemblages. In addition, we conclude that there is patterned variability in the ways that VE accumulate and modify the bones of their prey. There are two

distinct skeletal-parts preservation, bone breakage, and bone surface modification patterns among the prey in our sample: one that characterizes hyraxes, mole-rats, and carnivores, and another that characterizes hares and bovids. Faunal analysts investigating the potential role of VE at fossil sites should be aware of 1) these taphonomic patterns and differences and 2) that there is no singular pattern of accumulation. We define patterns of preservation, breakage, and bone modification that can be employed on a taxon-specific basis to distinguish VE prey remains from other bone accumulators.

1 – INTRODUCTION

Over the last 30 years, taphonomy has played a central role in our improved understanding of the natural and cultural processes involved in the formation of fossil assemblages. To this end, actualistic and experimental studies have been instrumental in developing the criteria used to characterize the signatures of several bone accumulating agents (Binford, 1981; Bonnichsen and Sorg, 1989; Brain, 1981; Domínguez-Rodrigo and Piqueras, 2003; Domínguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Hudson, 1993; Landt, 2007; Marean et al., 1992; McGraw et al., 2006; Munro and Bar-Oz, 2005; Pickering et al., 2005; Pickering and Wallis, 1997; Pobiner et al., 2007; Sanders et al., 2003; Thompson and Henshilwood, 2014). The bulk of this research has focused on carnivorous mammals and humans, and though raptors have been recognized as

accumulators of fossil bone (Andrews, 1990; Berger and Clarke, 1995; Fernández-Jalvo et al., 1998; Gilbert et al., 2009; Klein and Cruz-Uribe, 2000; Lloveras et al., 2011; Sampson, 2000), the criteria used to characterize the signatures of their involvement and the range of variability within those signatures remain less-well defined.

This variability is especially true of diurnal raptors such as eagles. Some eagle predation studies (Bochenski et al., 2009; Erlandson et al., 2007; Hockett, 1995; 1996; McGraw et al., 2006; Sanders et al., 2003; Schmitt, 1995; Trapani et al. 2006) have documented fairly minimal levels of damage to eagle prey remains, while other studies (Andrews, 1990; Bochenski et al., 1997; Brain, 1981; Cruz-Uribe and Klein, 1998; Hoffman, 1988; Lloveras et al., 2008a; Msuya, 1993) have noted considerable bone modification and patterning. This suggests that different eagle taxa capture, consume, and transport their prey in distinctive ways, perhaps depending on the size and/or predator-avoidance behavior of the prey as well as the hunting adaptations of specific eagle taxa. Thus, it is clear that a uniform signature of predation that encompasses all eagle taxa is unlikely to exist.

The specific goals of this paper are to describe the mammalian prey composition and taphonomic signatures of Verreaux's eagle (*Aquila verreauxii*). Verreaux's eagle (VE) is a major accumulator of mammal bone in parts of Africa and its potential contribution to Stone Age fossil sites has been recognized

(Brain, 1981; Cruz-Uribe and Klein, 1998). Distinguishing between the bones accumulated by different agents such as diurnal raptors, owls, carnivores, and humans is essential to gaining an understanding of human subsistence activity. Consequently, there is a need to distinguish the signatures of VE agency with as much precision as possible as they often roost in and around rock shelters and caves, locations that attract other bone accumulators, including humans. In addition, VE routinely hunt and scavenge prey that other raptors, humans, and carnivorous mammals also target, such as leporids, large rodents, and small bovids. Because of these factors, precise criteria are needed in order to determine what role VE may have played, if any, in the accumulation of bones at fossil sites. This contribution is part of a wider study aimed at elucidating the roles of avian raptors and anatomically modern humans at Die Kelders Cave 1 and Pinnacle Point site 5-6 (Armstrong, A. in prep.).

2 – Verreaux's eagle general habits

VE is a large (male 3.7 kg, female 4.5 kg; wingspan 2.0-2.8 m; height 80-96 cm) diurnal bird of prey that inhabits rocky hill, gorge, and mountain habitats (Hockey et al., 2005). Their distribution is broad, ranging from the Arabian Peninsula to eastern and southern Africa and is generally restricted to areas where annual rainfall is <750 mm (Hockey et al., 2005). The highest

concentrations of VE are found along the mountains of Ethiopia, the highlands of Chad, Angola, Zimbabwe, and South Africa (SA) (Hockey et al., 2005).

VE hunt aerially or from a perch, utilizing stealth and speed to surprise their prey (Gargett, 1990; Hockey et al., 2005). They have also been observed to scavenge carrion and steal prey from other raptors (Gargett, 1990; Steyn, 1982). VE often hunt in pairs (Steyn, 1982). Jenkins (1984) estimated VE's predation rate at 1 kill/30 hours. Gargett (1990) approximates that at Matopos Hills, Zimbabwe, where a pair of eagles and their eaglet accounted for ~400 hyraxes in a year. By quantifying the prey remains from 73 nest sites in SA, Boshoff et al. (1991) observed that mammals are the primary target of VE – comprising between 81-90% of the diet – followed by birds and reptiles. They generally prey on smaller mammals weighing between 1-14 kg with an average weight of ~3.5 kg (Hockey et al., 2005) but have been known to take animals up to 20 kg in weight (Steyn, 1982). In SA, rock hyraxes (*Procavia capensis*) frequently constitute between 40-90% of the diet (Boshoff et al., 1991; Davis, 1994). This eagle always builds its nests on steep, inaccessible cliffs, rarely in trees (Hockey et al., 2005; Steyn, 1982).

Other common prey taxa include lagomorphs (*Lepus* spp. and *Pronolagus* spp.), large rodents (*Bathyergus suillus* and *Hystrix africaeaustralis*), small bovids (*Raphicerus* spp., *Oreotragus oreotragus*, and a variety of juvenile antelopes), small carnivores (*Felis sylvestris, Cynictis penicillata,* mongooses,

and genets*)*, and primates (galagos Family: Galagidae), *Papio ursinus* and *Chlorocebus spp.* (monkeys)) (Boshoff et al., 1991; Davis, 1994; Gargett, 1990; Hockey et al., 2005; Steyn, 1982; Zinner and Paláez, 1999). Of their larger mammalian prey (e.g. *H. africaeaustralis, P. ursinus*, and antelopes) juveniles tend to be favored (Davis, 1994; Zinner and Paláez, 1999). VE have been reported to scavenge on the remains of large adult mammals such as baboons, zebra, domestic cattle, sheep and goats, and large antelope, bones of which have been occasionally recovered from nest sites (Boshoff et al., 1991; Gargett, 1990; Steyn, 1982). Boshoff et al. (1991) and Gargett (1990) found that medium- to large-sized birds such as Helmeted Guineafowl (*Numida meleagris* and *Guttera eduardi*), francolins and spurfowl (*Francolinus* and *Pternistis* spp.), and bustards (Family: Otididae) are the most common avian prey of VE in southern Africa. Occasionally reptiles like tortoises (common in some areas), snakes, and lizards (especially *Varanus* spp.) are taken (Hockey et al., 2005).

3 – MATERIALS AND METHODS

3.1 - Study sample

Our study sample consists of prey remains recovered from the area below five nest sites and adjacent feeding perches located in the Cape Floral Region (Figure 1). All material was collected in discrete phases per nest site between 1988 and 2000; the sample was selected for study as (1) systematic collection at

the nest sites and adjacent feeding perches was regularly conducted, (2) the collection criteria included the gathering of all prey remains (undigested bones, fresh and degraded pellets, tortoise, bird and gastropod shell, feathers and fur), and (3) the collections afforded an ample representative sample that could be prepared and studied within a reasonable time-frame. The deposits below the sites were not screened; however, the fact that many small specimens such as teeth and podial bones were collected offers the assurance that the sample accurately reflects the catchment of bone from the nests. The actual nests were not checked for bones as they were built on steep cliffs and inaccessible. However, as is the habit with many birds of prey (Gargett, 1990 and Hockey et al., 2005), old bones are periodically cleaned out from the nest and, since the collections were regularly made, much of the potential bias was likely mitigated. In a current study of VEs in the Western Cape Province, M. Murgatroyd (Animal Demography Unit, University of Cape Town, pers. comm.) has observed that some, but not all, nests she accessed had bones on them, but that this would not affect the composition of samples below. In addition to undigested prey remains, a total of five pellets were recovered from the nests and feeding perches.

The specimens required cleaning in order to identify and expose the bone surfaces. Rinsing with cool tap water and agitation with one's fingers was usually sufficient to remove debris. Removal of any remaining tissue was achieved after soaking for four hours in room temperature water. Where implements were required, wooden tools and soft-bristled brushes were used to avoid damage to

the specimens. The specimens were not handled again until they were dry. Pellets were broken up by hand and the bones were removed with the aid of forceps. The digested bones were extremely fragile and not rinsed or brushed.

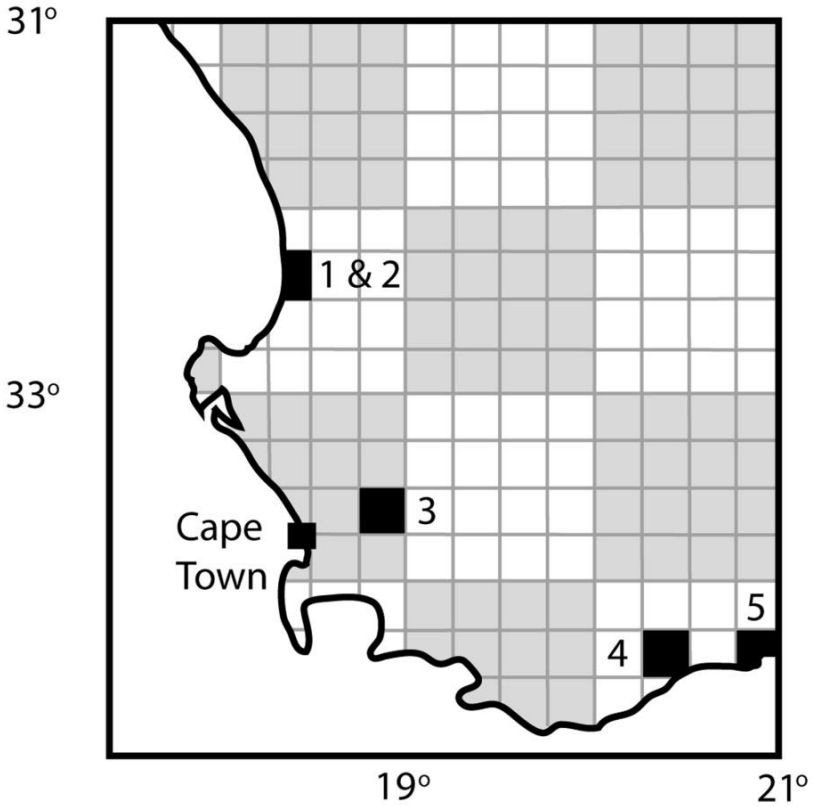


Figure 1. Location within quarter degree squares of the nest sites from which the Verreaux's eagle samples were collected: 1-Baboon Point; 2-Verlorenvlei; 3-Agter Paarl; 4-Bloukrans; 5-Windhoek.

3.2 - Taxonomic and skeletal element representation

Skeletal element and taxonomic identifications were made with the aid of the Museum's comparative osteological collection. We recorded the portion of bone preserved and orientation of paired elements. We attempted to identify all

specimens, regardless of size, to the highest taxonomic level possible. Taxa cited are from Skinner and Chimimba (2005) and Hockey et al. (2005) for mammals and birds respectively. Most specimens could be identified to a specific skeletal element but a small number of fragmentary specimens lacked diagnostic features and were identified as undifferentiated mammal, bird, reptile, or unidentifiable bone. Most of the undifferentiated specimens are <3mm in maximum dimension. The vast majority of vertebrate remains were identified to genus and most of these were identifiable to species. However, some bovid specimens could only be identified to size class 1 or 2 of Brain's (1981) bovid size categories. As there were multiple species of hares, bovids, and carnivores identified, these taxa have been grouped in their own respective categories for analytical purposes.

For mammal remains, skeletal element fragmentation was recorded following a method for small mammals described by Lloveras et al. (2008a). This detailed method allows for comparison of skeletal-part frequencies of similar small mammal accumulations and facilitates aggregation of element categories for comparison with other data sets. To estimate skeletal-part frequencies, we calculated the Relative Abundance (RA) of each skeletal element by taxa as defined by Andrews (1990). RA is our preferred method of assessing and comparing skeletal-part frequencies as a number of small mammal assemblages have been reported in this way (Andrews, 1990; Cochard, 2004; Lloveras et al, 2008a; 2008b; 2009; McGraw et al., 2006; Rodríguez-Hidalgo et al, 2013;

Sanders et al, 2003; Trapani et al., 2006). We have also calculated percent Minimum Number of Individuals (MNI) and percent Minimum Animal Units (MAU) estimates to facilitate comparisons between other small mammal data sets (Cochard, 2008; Cruz-Uribe and Klein, 1998; Hockett, 1991; 1995; Munro and Bar-Oz, 2005).

3.3 - Bone density

To investigate the role of bone structural density in the patterning of prey skeletal-parts we used the closest available bone density values of taxa of similar size and build as density estimates for the prey taxa in our assemblage are not available. For hare and bovid bone density values we substituted *Lepus californicus* (Pavao and Stahl; 1999) and *Ovis aries* (Ioannidou, 2003) respectively. For the mole-rats, hyrax, and small carnivores we used the estimates for *Marmota monax* presented in Lyman et al. (1992). These bone estimates were derived by measuring bone density at specific scan sites on the skeleton using photon densitometry. The bone volume density estimates include both the mineral content and the bone volume measured at the scan site. Though performed on different taxa, the methods and calculations used to derive the bone density values are comparable across the density estimates. Preferably, we would have utilized bone density estimates obtained from computed tomography or photon densitometry that accounts for variation in the shape of bone cross-sections (Lam and Pearson, 2005; Lam et al, 2003).

However, we are limited by (1) the number of available comparable datasets, (2) the need to apply density estimates that accurately represent the taxa in our sample, and (3) the methodological necessity of employing density estimates that were obtained with comparable techniques.

3.3 - Age and Sex

Rock hyraxes (*Procavia capensis*): We recorded the dental eruption and wear stages of mandibular and maxillary specimens and categorized each based on the rock hyrax eruption and wear schedule devised by Steyn and Hanks (1983). Boshoff et al. and Cruz-Uribe and Klein (1998) established these hyrax eruption states can be employed to group neonates, juveniles, subadults, and adults. We present eruption data on mandibular specimens only as: (1) mandibles are better represented than maxillae and (2) we assume that many of the mandibles and maxillae originate from the same individuals. Hyraxes are sexually dimorphic and can be accurately sexed based on the shape of the upper incisor and incisor alveoli (Thomas, 1892).

Cape dune mole-rats (*Bathyergus suillus*): Maxillae with *in situ* cheek teeth can be meaningfully grouped into relative age cohorts (neonate, juvenile, subadult, and adult) based on the dental eruption and wear pattern scheme described by Hart et al. (2007), a methodology similar to those employed by Avery (1990) and Klein and Cruz-Uribe (2000). As with many other rodent species, *B. suillus* is born with some permanent dentition, the P4 and M1, in

place (Bennett and Faulkes, 2000). Near the weaning period – 21 days after birth – M2 begins to erupt (Jarvis and Bennett, 1991). The tooth is visible by the time the pup disperses from the nest between 60-65 days after birth (Jarvis and Bennett, 1991) and is in full occlusion sometime thereafter. After the pup disperses from the nest and M2 is in or near occlusion, M3 begins to erupt (J.U.M. Jarvis, University of Cape Town, pers. comm.). Based on this schedule and the Hart et al. (2007) tooth-wear and eruption descriptions, we have assigned their tooth-wear and eruption classes to these age cohorts: class 1 = neonates, classes 2-3 = juveniles, classes 4-5 = subadults, and classes 6-9 = adult. At present, a method to accurately sex mole-rat skeletal remains does not exist (though a technique is forthcoming [Montoya-Sanhueza et al, 2013]).

Hares (*Lepus* spp.): As cranial specimens and dentitions are scarcely represented in our hare sample, we follow Hockett (1991, 1995) and Cruz-Uribe and Klein (1998) and present hare postcranial fusion data to provide some information about prey age. Where it can be determined, hares have been divided into adult or juvenile specimens. Sex determination for hares was unattainable.

Bovids (*Family: Bovidae*): We use Hillson's (2005) bovid dental eruption scheme to ascertain age. Hillson depicts and describes four bovid dental eruption categories based on a series of domestic sheep mandibles; because six of our mandibles are *Ovis/Capra* spp. and our sample size is small, we use

Hillson's categories to assess all bovids in our assemblage. The age categories are: neonate = deciduous dentition, with deciduous third and fourth premolars erupted and in wear, permanent first molar may be in early stages of eruption; juvenile = mixed dentition, with deciduous third and fourth premolars still present, permanent first molar fully erupted and in wear, and second molar still erupting; subadult = permanent cheek teeth almost complete, with third molar in eruption; adult = full set of permanent cheek teeth, with the third molar in wear. Few well-preserved bovid cranial specimens were recovered making it difficult to ascertain a sex ratio.

Carnivores: Age assessment criteria for the carnivores in our assemblage do not exist. However, it is possible to provide some information about prey age as several maxillae and mandibles with complete dentitions were preserved as well as long bone epiphyses. Sex ratio determination was not possible given the lack of established methods to determine carnivore sex.

3.4 - Surface modifications

All specimens were inspected with a 10-40x binocular zoom microscope under high incident light to examine for and document surface modifications. Bone damage was identified and recorded according to previously-published criteria. Taphonomic indicators such as weathering (Andrews, 1990; Behrensmeyer, 1978), rodent gnawing (Brain, 1981), and post-depositional surface alterations (Thompson, 2005) were recorded but were seldom observed

given the collection's modernity and thus lack of exposure. Digestive alteration to teeth and bones was observed and recorded after a system devised by Andrews (1990) and summarized by Lloveras et al. (2008a).

Damage categories were recorded using criteria adopted from established sources in the taphonomic literature; characterization, frequency and location of punctures (Andrews, 1990; Binford, 1981; Blumenschine et al., 1996; Brain, 1981; Elkin and Mondini, 2001; Hockett, 1991, 1995; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al. 2007; Sanders et al., 2003; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014; Trapani et al., 2006), pits (Binford, 1981; Blumenschine and Selvaggio, 1988; Blumenschine et al., 1996; Domínguez-Rodrigo and Piqueras, 2003; DomÍnguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al. 2007; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014), scores (Binford, 1981; Blumenschine et al., 1996; Bunn, 1981; Elkin and Mondini, 2001; Haynes, 1980; 1982; 1983b; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al., 2007; Sanders et al., 2003; Shipman, 1981; Shipman and Rose, 1983; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014; Trapani et al., 2006), notches (Binford, 1981; Blumenschine and Selvaggio, 1991; Brain, 1981; Capaldo and Blumenschine, 1994; Domínguez-Rodrigo et al., 2013; Fisher, 1995; Haynes, 1982; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al., 2007), crenulated (Binford, 1978, 1981; Brain, 1981; Domínguez-Rodrigo et al.,

2013; Elkin and Mondini, 2001; Fisher, 1995; Lyman, 1994; Pickering and Wallis, 1997; Landt, 2007) and fractured edge (Binford, 1981; Domínguez-Rodrigo et al., 2013; Johnson, 1985; Landt, 2007; Pickering and Wallis, 1997) were recorded according to previously-published criteria.

3.5 – Fragmentation

To determine whether the bones were fractured when fresh, the morphology of the fracture angle, fracture outline, and fracture edge were recorded for all long bone shaft fragments following Villa and Mahieu (1991). As comparable small mammal bone breakage data does not exist, we compared our breakage data to the French Neolithic sites studied by Villa and Mahieu. The sites are a suitable comparison as the Fontbrégoua collection was fractured when fresh and Sarrians was broken when dry.

3.6 - Specimen and feature measurements

The maximum length and width of each specimen was measured using digital calipers. To estimate bone puncture size, we measured and recorded the length and width at the maximum dimensions and together with the shape of the puncture, size was calculated in millimeters squared. Most punctures were easily categorized into one of four shapes: circular, oval, rectangular, or triangular. Punctures that could not be defined as such were categorized as irregular. Maximum notch breadth was measured parallel to the fracture edge

after Capaldo and Blumenschine (1994). All measurements were rounded to the nearest tenth of a millimeter.

3.7 - Statistical analysis

We used hierarchical cluster analysis (Neff and Marcus, 1980; Romesburg, 1984) in order to determine which taxa are similar with respect to (1) skeletal-part representation and (2) bone fragmentation. For each of these two variables the values of the resemblance coefficients are arranged in dendrograms representing the hierarchy of similarities among the taxa. In addition, we use principal components analysis to verify the strength of the cluster analyses (Podani, 1994) and report the total variance attributable to each cluster. Binomial logistic regression analysis (Hosmer et al, 2013) was used with respect to (1) bone fragmentation and (2) bone surface modification due to their dichotomous nature (i.e. two possible values, modified or not). This multivariate procedure permits the discovery of complex relationships between one or more dependent categorical variables (fragmentation and surface modification) and a set of nominally scaled independent variables (taxa and skeletal elements) and is used to identify independent variables that are significantly associated with the dependent variable. All statistical analyses were performed with the software program R, version 2.15.3.

4 - RESULTS

4.1 - Prey composition

We identified 3532 (n) specimens from the VE nests, of which 3413 (NISP) were identifiable to skeletal element and taxon (Table 1). The specimens represent no fewer than 421 (MNI) individuals from at least 19 different taxa. Of the 421 individuals identified, 371 (88.1%) were mammals, 25 (5.9%) were tortoises, 24 (5.7%) were birds, and one (0.1%) was a fish. Based on MNI the most common prey taxa are rock hyraxes (45.8%), Cape dune mole-rats (25.7%), hares (8.8%), tortoises (5.9%), bovids (3.3%), small carnivores (3.3%), pigeons (2.6%), followed by swifts and starlings (1.4%). Included in these counts are 14 (NISP) specimens retrieved from five pellets.

A small portion of the assemblage could not be identified to a specific taxon or skeletal element: 37 n (1.0%) are undifferentiated mammal, 26 n (0.7%) are undifferentiated bird, 27 n (0.7%) are undifferentiated tortoise, and 29 n (0.8%) are undifferentiated indeterminate bone. All undifferentiated bone was excluded from further analysis since such material is likely to derive from identified individuals.

Table 1. The taxa represented in the Verreaux's eagle nest sites (NISP=number of identified specimens; MNI=minimum number of individuals).

Species	NISP	MNI	% NISP	% MNI
Mammals	**2974**	**371**	**87.1%**	**88.1%**
Procavia capensis (Rock hyrax)	1497	193	43.9%	45.8%
Bathyergus suillus (Cape dune mole-rat)	710	108	20.8%	25.7%
Lagomorphs	595	37	17.4%	8.8%
Lepus capensis (Cape hare)	119	7	3.5%	1.7%
Lepus saxatilis (Scrub hare)	144	13	4.2%	3.1%
Lepus spp. (hares)	332	17	9.7%	4.0%
Bovids	104	14	3.0%	3.3%
Raphicerus spp. (Grysbok/steenbok)	23	5	0.7%	1.2%
Ovis/Capra spp. (Sheep/goat)	16	4	0.5%	1.0%
Bovid size 1	37	3	1.1%	0.7%
Bovid size 2	28	2	0.8%	0.5%
Carnivores	54	14	1.6%	3.3%
Genetta spp. (Genet)	2	1	0.1%	0.2%
Herpestes ichneumon (Large grey mongoose)	1	1	0.0%	0.2%
Galerella pulverulenta (Cape grey mongoose)	51	12	1.5%	2.9%
Micro mammal	14	5	0.4%	1.2%
Otomyinae indet.	4	4	0.1%	1.0%
Micro mammal indet.	10	1	0.3%	0.2%
Birds	**177**	**24**	**5.2%**	**5.7%**
Columba spp. (Pigeons)	91	11	2.7%	2.6%
Raptors	54	3	1.6%	0.7%
Aquila sp. (Large eagle) cf *A. verreauxi*	52	2	1.5%	0.5%
Bubo africanus (Spotted eagle-owl)	2	1	0.1%	0.2%
Swifts and starlings	20	6	0.6%	1.4%
Onychognathus morio. (Red-winged starling)	15	5	0.4%	1.2%
Tachymarptis melba (Alpine swift)	5	1	0.1%	0.2%
Galliformes	12	4	0.4%	1.0%
Franolinus/Pternistis spp. (Francolin/spurfowl)	3	1	0.1%	0.2%
Numida meleagris (Helmeted guineafowl)	9	3	0.3%	0.7%
Tortoise	**257**	**25**	**7.5%**	**5.9%**
Chersina angulata (Angulate tortoise)	257	25	7.5%	5.9%
Fish	**5**	**1**	**0.1%**	**0.2%**
Undifferentiated				
Mammal	37	-	-	-
Bird	26	-	-	-
Tortoise	27	-	-	-
Indet. bone	29	-	-	-
Total NSP	3532	-	-	-
Total NISP	**3413**	**421**	-	**99.9**

4.1.1 - Mammals

Mammals represent the largest prey class recovered from the VE nest sites, accounting for 2974 NISP (87%). Over 97% of the mammal bones were identified to at least the level of genus and all are terrestrial species. The remains of at least 10 different mammalian taxa were identified, comprising an MNI of 371. Small mammals (those weighing between 500g and 4.5kg adult body weight) dominate the assemblage with 2856 NISP (84%) and 352 MNI (84%). Bovid size classes 1 and 2 are represented by 60 NISP (1.8%) and 8 MNI (1.9%), and 44 NISP (1.3%) and 6 MNI (1.4%) respectively. Micromammals (<500g adult body weight) are represented by 14 NISP (0.4%) and 5 MNI (1.2%).

Rock hyraxes: Hyraxes are the most abundant prey in the VE sample with 1479 NISP (43.9%) and 193 MNI (45.8%). Of the specimens that could be sexed, 46 (45.1%) were females and 56 (54.9%) were males. Of the mandibles that could be aged, 9 (5%) are neonates, 35 (18%) juveniles, 48 (25%) sub-adults and 101 (52%) adults.

Cape dune mole-rats: Mole-rat remains account for 710 NISP (20.8%) and 108 MNI (25.7%) in our assemblage. Of the maxillae that could be aged, adults are the dominant cohort in the assemblage: 0 neonates, 2 juvenile, 6 sub-adult, and 45 adult.

Hares: We identified Cape hare (*Lepus capensis*) and scrub hare (*L. saxatilis*) but did not find Smith's red rock rabbit (*Pronolagus rupestris*) in our

prey assemblage. Hares account for 595 NISP (17.4%) and 37 MNI (8.8%) of the assemblage. Hare remains are dominated by adult individuals as the vast majority of humeri (85.7%) and tibiae (80.4%) are fused at both the proximal and distal ends.

Bovids: Bovid skeletal remains are represented in the assemblage by 104 NISP (3.0%) and 14 MNI (3.3%). We identified *Raphicerus* spp. and *Ovis/Capra* spp. as well as specimens that could only be identified to either bovid size class 1 or 2. We found only one adult mandible (8%); all others were classified as sub-adults or younger (92%). Juveniles are the most abundant age-class, accounting for 62% of the aged mandibles.

Carnivores: At least three small carnivore species are present: *Genetta* spp., *Herpestes ichneumon,* and *Galerella pulverulenta*. As a group they account for 54 NISP (1.6%) and 14 MNI (3.3%). All of the small carnivore cranial specimens exhibit fully-erupted adult dentitions in varying degrees of wear; there are no sub-adult cranial specimens in the sample. In addition, all carnivore long bones are fused at the proximal and distal ends.

4.2 - Skeletal-Part Representation and Survivorship

Percent RA, MNI, and MAU are presented in Table 2 and Figure 2. It should be pointed out that because our MNE values were summed over five

separate nest sites, there are no RA values for hares, bovids, or carnivores that reach 100%. Figure 3 provides a hierarchical cluster diagram of the five prey aggregates arranged by similarities in skeletal-part representation, while Table 3 contains the principal component values for the comparisons between the skeletal-part frequencies of each prey taxa. Our cluster analysis indicates that there are two patterns of skeletal-part preservation among the five mammalian prey aggregates. While bearing in mind differences in sample size, it appears that hyrax, mole-rat and carnivore bones are similarly differentially preserved and differ from the skeletal-part pattern of hares and bovids. Our principal components analysis supports the cluster analysis as PC1 has the largest loadings for hyrax, mole-rat, and carnivore. These taxa are approximately equal and they explain 68.5% of the variation in the data. The second PC explains almost all the remaining variation as PC2 loads for hares and bovids.

Table 2. Minimum number of elements (MNE), percent relative abundance (%RA), percent minimum number of individuals (%MNI), and percent minimum animal unit (%MAU) values for the mammals recovered from the Verreaux's eagle nests.

	Hyrax				Mole-rat				Hare				Bovid				Carnivore			
Skeletal element	**MNE**	**%RA**	**%MNI**	**%MAU**	**MNE**	**%RA**	**%MNI**	**%MAU**	**MNE**	**%RA**	**%MNI**	**%MAU**	**MNE**	**%RA**	**%MNI**	**%MAU**	**MNE**	**%RA**	**%MNI**	**%MAU**
Crania (Maxilla)	352	91%	93%	94%	209	97%	100%	100%	11	15%	16%	19%	3	11%	33%	23%	22	79%	100%	100%
Mandible	373	97%	100%	100%	111	51%	56%	53%	2	3%	5%	3%	13	46%	100%	100%	10	36%	50%	45%
Incisors (iso.)	54	5%	6%	0%	5	1%	4%	0%	9	6%	14%	0%	0	0%	0%	0%	0	0%	0%	0%
Up ck. teeth (iso.)	12	0%	1%	0%	16	2%	5%	0%	0	0%	0%	0%	0	0%	0%	0%	2	3%	8%	0%
Low ck. teeth (iso.	12	1%	1%	0%	9	1%	5%	0%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%
Atlas	4	2%	2%	2%	0	0%	0%	0%	0	0%	0%	0%	1	7%	11%	15%	0	0%	0%	0%
Axis	1	1%	1%	1%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%
Cervicals	10	1%	1%	1%	3	0%	1%	1%	2	1%	3%	1%	1	1%	11%	3%	0	0%	0%	0%
Thoracics	24	1%	2%	1%	2	0%	1%	0%	13	3%	5%	4%	0	0%	0%	0%	0	0%	0%	0%
Lumbars	35	3%	3%	2%	9	0%	3%	1%	85	33%	38%	41%	0	0%	0%	0%	0	0%	0%	0%
Caudal	9	1%	1%	0%	2	0%	1%	0%	0	0%	0%	0%	0	0%	0%	0%	0	0%	0%	0%
Sacrum	4	2%	2%	2%	3	0%	3%	3%	20	54%	54%	68%	0	0%	0%	0%	0	0%	0%	0%
Ribs	12	0%	1%	0%	4	0%	1%	0%	8	1%	5%	1%	2	1%	11%	1%	0	0%	0%	0%
Scapula	27	7%	8%	7%	3	1%	2%	1%	1	1%	3%	2%	1	4%	11%	8%	0	0%	0%	0%
Humerus	26	7%	8%	7%	20	12%	11%	10%	10	14%	22%	17%	8	18%	44%	38%	4	14%	25%	18%
Radius	7	2%	2%	2%	3	1%	3%	1%	12	16%	22%	20%	2	7%	11%	15%	1	4%	8%	5%
Ulna	3	1%	1%	1%	17	8%	10%	8%	9	12%	16%	15%	3	300%	22%	15%	2	7%	17%	9%
Metacarpal	3	0%	1%	0%	0	0%	0%	0%	0	0%	0%	0%	5	14%	33%	31%	0	0%	0%	0%
Pelvis	163	42%	46%	44%	34	16%	22%	11%	59	80%	100%	100%	5	18%	56%	38%	2	7%	8%	9%
Femur	32	8%	11%	9%	26	15%	13%	12%	26	35%	41%	44%	8	29%	44%	62%	3	11%	17%	14%
Patella	4	1%	1%	1%	1	0%	1%	0%	1	1%	3%	2%	1	4%	11%	8%	0	0%	0%	0%
Tibia	16	4%	6%	4%	37	17%	21%	18%	53	71%	89%	90%	8	29%	67%	62%	3	11%	17%	14%
Fibula	6	2%	2%	2%	-	-	-	-	-	-	-	-	2	7%	22%	15%	1	4%	8%	5%
Calcaneus	7	2%	3%	2%	6	3%	5%	3%	16	22%	32%	27%	2	7%	22%	15%	2	7%	8%	9%
Astragalus	10	3%	4%	3%	3	1%	2%	1%	15	20%	30%	25%	2	7%	22%	15%	0	0%	0%	0%
Carpals/tarsals	0	0%	0%	0%	0	0%	0%	0%	2	3%	5%	0%	1	0%	11%	8%	0	0%	0%	0%
Metatarsals	14	2%	2%	1%	8	1%	3%	1%	46	16%	22%	19%	3	11%	22%	23%	0	0%	0%	0%
Phalanx 1/2	22	0%	1%	0%	3	0%	2%	0%	54	4%	24%	5%	5	2%	22%	5%	0	0%	0%	0%
Phalanx 3	1	0%	1%	0%	9	0%	4%	0%	27	4%	24%	5%	0	0%	0%	0%	0	0%	0%	0%

Table 3. Principal component values for comparisons between (1) skeletal-part frequencies and (2) fragmented and whole bones of hyraxes, mole-rats, carnivores, bovids, and hares.

Importance of components:	PC1	PC2	PC3	PC4	PC5
(1) Standard deviation	0.3628	0.2148	0.09731	0.06976	0.01171
(1) Proportion of Variance	0.6847	0.2400	0.04925	0.02531	0.00071
(1) Cumulative Proportion	0.6847	0.9247	0.97398	0.99929	1.00000
(2) Standard deviation	1.6293	0.7439	0.43450	0.10660	0.07073
(2) Proportion of Variance	0.7778	0.1621	0.05531	0.00333	0.00147
(2) Cumulative Proportion	0.7778	0.9399	0.99520	0.99853	1.00000

The abundance of maxillae and mandibles among the hyraxes, mole-rats, and carnivores is particularly conspicuous in comparison to hares and, to lesser extent, bovids. Another striking pattern is the lack of most postcranial remains among the hyraxes, mole-rats, and carnivores, a notable exception being the relative frequency of preserved hyrax pelves. There is a tendency among all five prey groups for hind limb elements (pelvis, femur, and tibia) to outnumber forelimb bones (scapula, humerus, radius, and ulna) and for upper-limb (humerus and femur) to outnumber lower-limb elements (ulna, radius, and tibia), with different degrees of variation among the prey aggregates (Table 4). With the exception of hares, axial/torso bones (vertebrae, sacrum, and ribs) are minimally represented among the prey groups. Autopodial elements are scarce for all taxa.

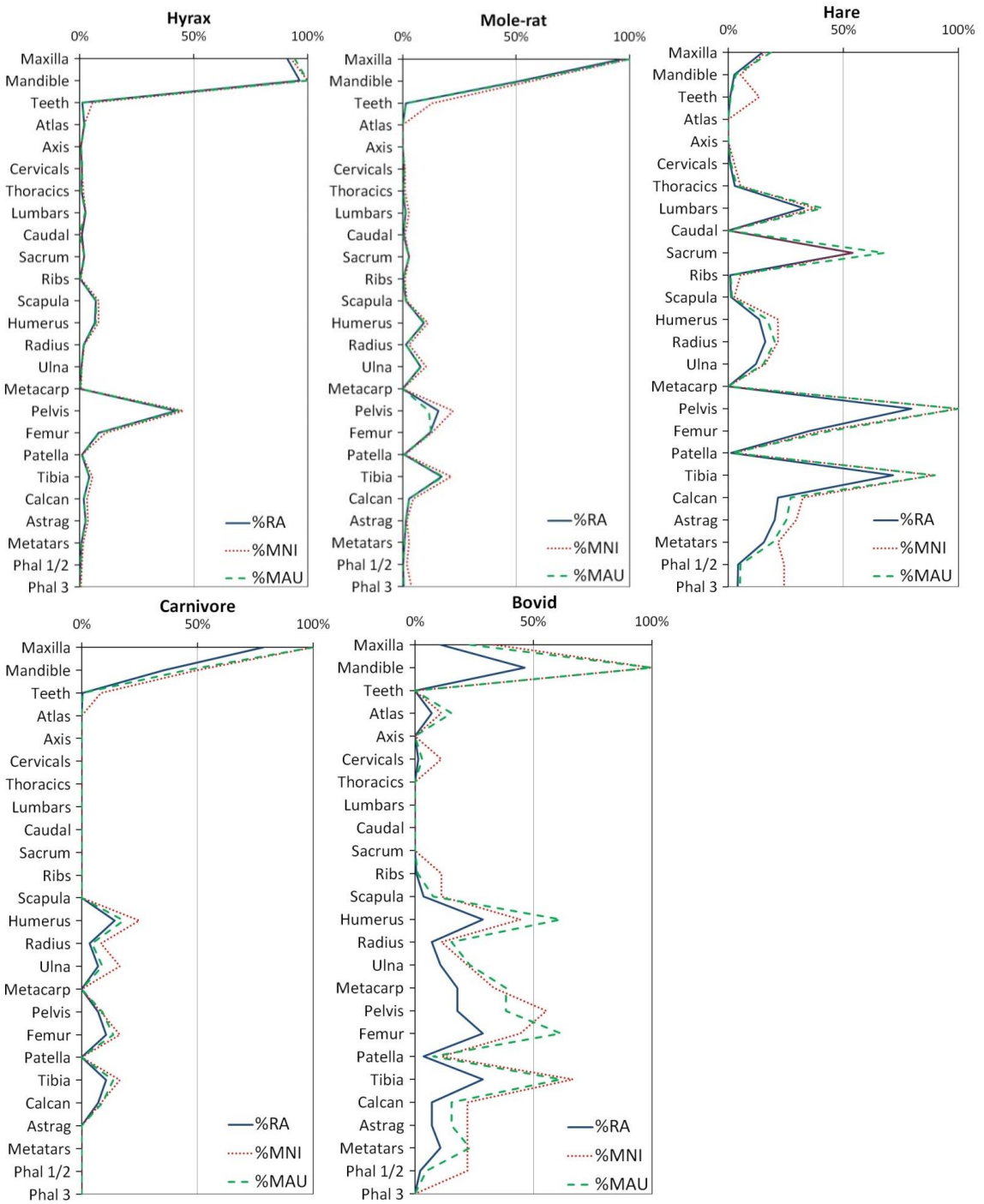


Figure 2. Skeletal part frequencies (bone survivability) of the mammal prey remains recovered from Verreaux's eagle nests. Full blue lines=%RA, dotted red lines=%MNI, and dashed green lines=%MAU.

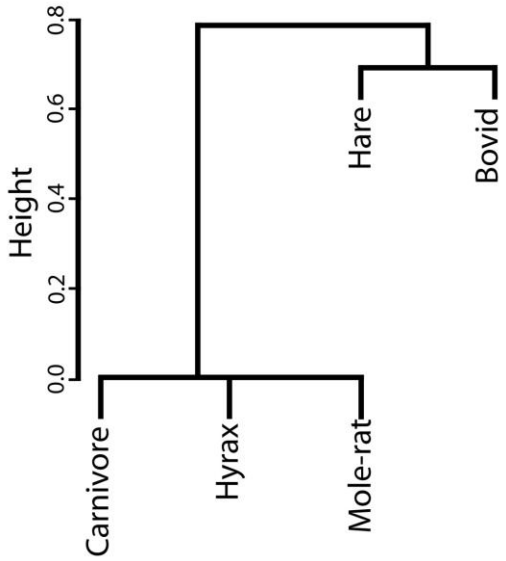


Figure 3. Cluster dendrogram summarizing the similarities in skeletal-part representation of the mammals recovered from the Verreaux's eagle nests.

The abundance of maxillae and mandibles among the hyraxes, mole-rats, and carnivores is particularly conspicuous in comparison to hares and, to lesser extent, bovids. Another striking pattern is the lack of most postcranial remains among the hyraxes, mole-rats, and carnivores, a notable exception being the relative frequency of preserved hyrax pelves. There is a tendency among all five prey groups for hind limb elements (pelvis, femur, and tibia) to outnumber forelimb bones (scapula, humerus, radius, and ulna) and for upper-limb (humerus and femur) to outnumber lower-limb elements (ulna, radius, and tibia), with different degrees of variation among the prey aggregates (Table 4). With the

exception of hares, axial/torso bones (vertebrae, sacrum, and ribs) are minimally represented among the prey groups. Autopodial elements are scarce for all taxa.

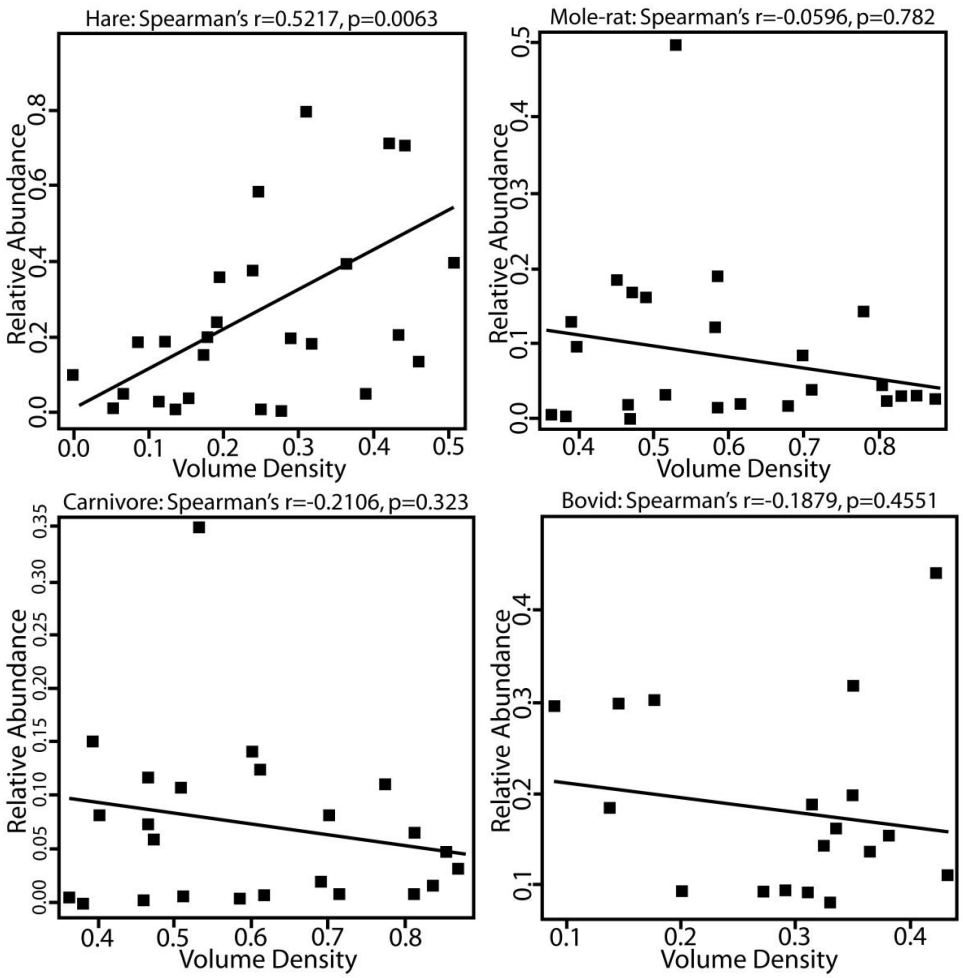
Table 4. Relative numbers of skeletal elements comparing proportions of postcranial to cranial elements (PC/C)[1], lower limb to upper limb elements (ZE/ST)[2], and anterior to posterior limb elements (AN/PO)[3] after Andrews (1990).

Indices	Hyrax	Mole-rat	Carnivore	Bovid	Hare
PC/C	13.6	17.8	21.9	62.5	353.8
ZE/ST	35.3	80.7	64.3	75.0	131.5
AN/PO	27.3	37.3	68.8	46.9	23.3

[1] Number of femur + humerus / mandibles + maxillae x 100.
[2] Number of tibia + (radius + ulna)/2 / femur + humerus x 100. Radius + ulna divided by 2 to correct for number of elements.
[3] Number of scapula + humerus + (radius + ulna)/2 / pelvis + femur + tibia x 100. Radius + ulna divided by 2 to correct for number of elements.

Of the five prey aggregates only hares (p=0.01; r_s=0.5217) have a significant, positive relationship between bone survivorship and bone structural density (Figure 4). For hyraxes (p=-0.23; r_s=0.273), carnivores (p=-0.21; r_s=0.323), mole-rats (p=-0.06; r_s=0.782), and bovids (p=-0.19; r_s=0.455) there is a weak, negative correlation between bone survivorship and density. None of these results are statistically significant, however. Conversely, four of the five prey aggregates exhibit positive and significant relationships between mean maximum dimension and bone survivorship (Figure 5). Hares (p=0.003, r_s=0.614), hyraxes (p=<0.001, r_s=0.704), mole-rats (p=<0.001, r_s=0.815), and bovids (p=0.007, r_s=0.616) all exhibit positive and significant relationships

between these attributes; only carnivores show a weak, negative correlation (p=0.387, r_s=0.308).



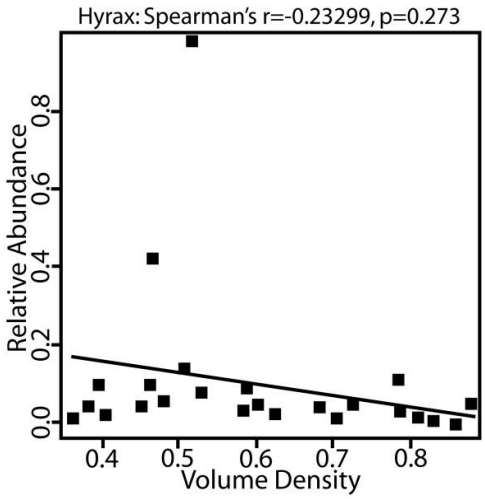


Figure 4. The relationship between bone density (volume density) and skeletal-element frequency (relative abundance) in the Verreaux's Eagle prey aggregates. Only hares have a positive and significant relationship between the two attributes. Hyraxes, mole-rats, carnivores, and bovids exhibit negative and non-significant relationships between bone density and skeletal-element frequency.

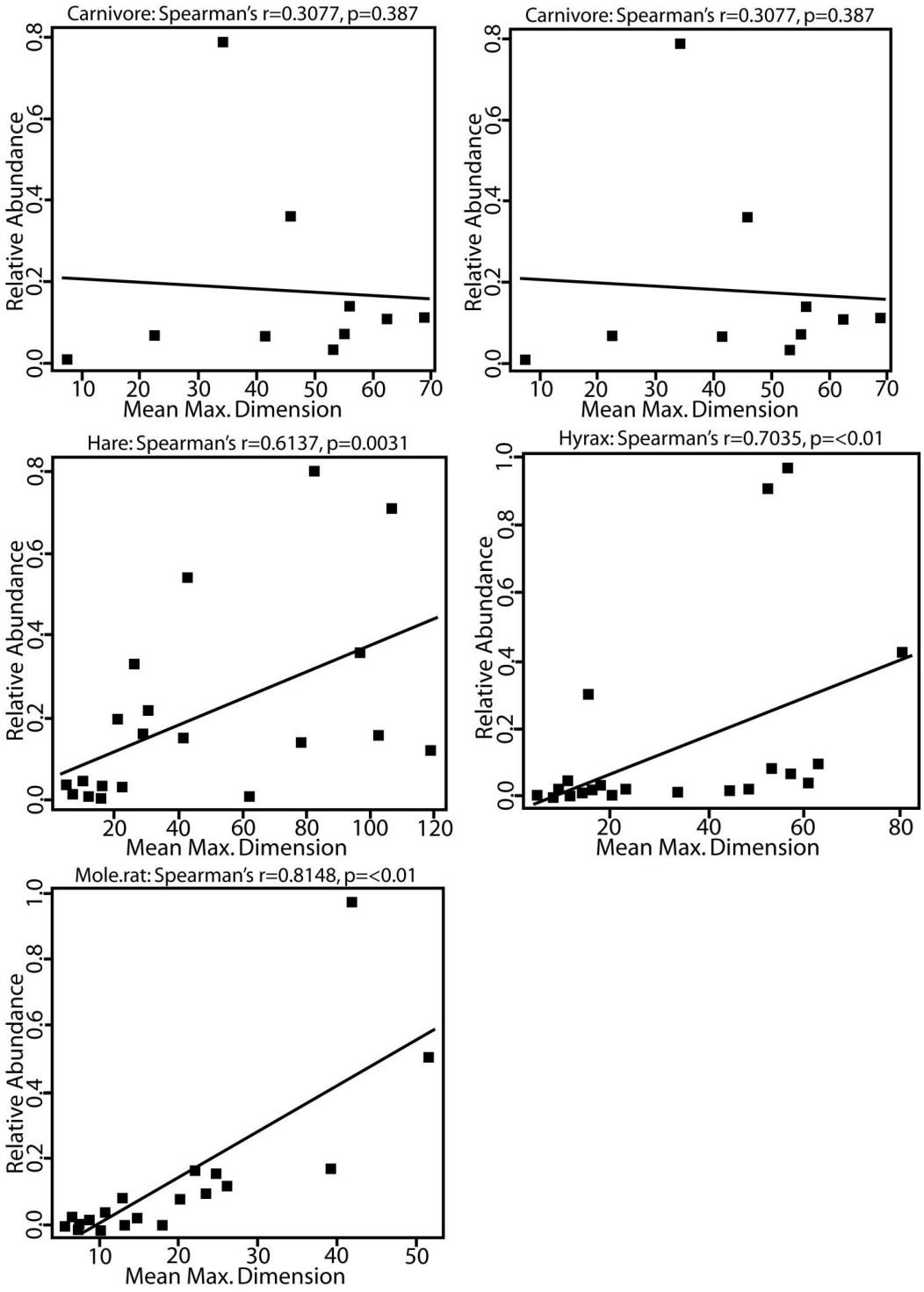


Figure 5. The relationship between mean maximum dimension of each skeletal element and skeletal-element frequency (relative abundance) of

the Verreaux's Eagle prey aggregates. All prey aggregates (except carnivores) exhibit a positive and significant relationship between the two attributes. Only carnivores have a negative and non-significant relationship between mean maximum dimension and skeletal-element frequency. Mean maximum dimension expressed in millimeters.

4.3 - Bone fragmentation and breakage

Our sample is dominated by long bones with oblique, v-shaped, and smooth breaks (Table 5). This breakage pattern typifies 'green' fracturing (Haynes, 1983a; Johnson, 1985; Villa and Mahieu, 1991). Nearly half of all mammal bones (45.9%) in the VE sample are broken (Table 6 and Figure 6) resulting in a fragmentation ratio of 1.23 (NISP: MNE). Predictably, small compact bones such as tarsals, patellae, and phalanges are among the most intact elements while more delicate bones such as ribs, scapulae, and crania are the least intact across all prey aggregates. Beyond these general observations, it is difficult to summarize across the assemblage as the degree of fragmentation varies by taxon and skeletal element.

Table 5. Occurrence of fresh and dry fracture angles, fracture outlines, and fracture edges for long bone shafts of the mammal prey aggregates from the Verreaux's Eagle assemblages.

	Fracture angle (%)			Fracture outline				Fracture edge	
	Oblique (fresh)	Right (dry)	Oblique /right	V-shaped (fresh)	Transverse (dry)	Inter-mediate	Transverse /curved	Smooth (fresh)	Jagged (dry)
Hyrax	59 (75)	11 (14)	8 (10)	56 (72)	9 (11)	1 (1)	12 (16)	67 (86)	11 (14)
Mole-rat	39 (89)	2 (5)	3 (6)	35 (79)	3 (7)	0 (0)	6 (14)	40 (92)	4 (8)
Carnivore	5 (90)	1 (10)	0 (0)	5 (90)	1 (10)	0 (0)	0 (0)	5 (90)	1 (10)
Hare	44 (72)	9 (15)	7 (13)	43 (72)	11 (18)	1 (1)	6 (9)	52 (86)	9 (14)
Bovid	14 (79)	3 (15)	1 (6)	15 (82)	1 (6)	0 (0)	2 (12)	14 (76)	4 (24)

To test for fragmentation differences we employed binomial logistic regression analysis, providing tests for differences between taxa adjusting for skeletal elements, and for skeletal elements adjusting for taxa (that is, Type II tests). The results indicate that the fragmentation differences between taxa (*Df*=4, *P*=0.03) and between skeletal elements (*Df*=24, *P*=<0.01) are significant at the 0.05 level (Table 7). To further investigate fragmentation similarities and differences between taxa, we used

Table 6. Bone fragmentation and specimen size data for the Verreaux's Eagle assemblage: percent whole bone (complete bone/NISP), fragmentation (NISP/MNE), mean, minimum, and maximum size of fragments measured in millimeters.

Skeletal Element	Hyrax					Mole-rat				Hare				Bovid				Carnivore			
	% Whole	Fragmentation	Mean Size	Min. Size	Max. Size	% Whole	Fragmentation	Mean Size	Min. Size	Max. Size	% Whole	Fragmentation	Mean Size	Min. Size	Max. Size	% Whole	Fragmentation	Mean Size	Min. Size	Max. Size	% Whole	Fragmentation	Mean Size	Min. Size	Max. Size
Crania	48.6	1.41	52.5	9.3	97.8	20.9	1.42	41.9	4.1	81.0	0.0	4.45	41.7	3.8	93.7	0.0	4.67	33.5	10.2	57.4	78.3	1.05	34.2	9.9	64.9
Mandible	44.7	1.10	56.8	8.0	83.5	55.9	1.31	51.7	4.6	76.0	0.0	4.00	15.9	5.4	30.4	43.8	1.23	133.4	46.2	174.6	70.0	1.00	45.9	35.5	50.5
Teeth	70.3	1.17	15.5	4.9	29.3	90.0	1.00	8.6	4.4	46.8	77.8	1.00	9.8	6.7	12.2	-	-	-	-	-	100.0	1.00	7.5	6.7	8.4
Atlas	50.0	1.00	23.4	18.5	26.2	-	-	-	-	-	-	-	-	-	-	100.0	1.00	25.9	25.9	25.9	-	-	-	-	-
Axis	100.0	1.00	17.9	17.9	17.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cervicals	60.0	1.00	11.2	5.5	20.1	100.0	1.00	9.8	6.1	13.7	0.0	1.50	7.5	5.1	9.9	0.0	1.00	32.0	32.0	32.0	-	-	-	-	-
Thoracics	63.0	1.13	11.2	4.2	22.9	50.0	1.00	7.5	7.5	7.6	73.3	1.15	22.5	8.7	32.3	-	-	-	-	-	-	-	-	-	-
Lumbars	54.3	1.00	15.4	4.1	27.9	77.8	1.00	7.2	7.0	75.0	63.6	1.04	26.4	7.1	43.6	-	-	-	-	-	-	-	-	-	-
Caudal	77.8	1.00	9.8	5.5	13.0	100.0	1.00	7.7	6.5	8.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sacrum	50.0	1.00	48.7	27.3	86.5	40.0	1.67	17.7	3.8	31.5	57.1	1.40	42.7	28.4	55.3	-	-	-	-	-	-	-	-	-	-
Ribs	16.7	1.00	10.8	3.3	30.0	7.7	3.25	13.2	8.7	17.7	18.2	1.38	14.6	8.6	24.4	0.0	1.50	84.1	64.0	122.3	-	-	-	-	-
Scapula	66.7	1.00	53.3	20.2	65.6	33.3	2.00	23.6	5.4	41.7	0.0	1.00	62.2	62.2	62.2	0.0	1.00	64.8	64.8	64.8	-	-	-	-	-
Humerus	50.0	1.23	57.6	8.3	78.0	75.0	1.20	26.1	7.8	47.3	81.8	1.10	78.7	20.1	94.9	70.0	1.25	75.3	41.9	99.6	100.0	1.00	56.0	49.1	62.2
Radius	66.7	1.29	44.8	8.1	68.7	50.0	1.33	7.9	3.2	29.5	83.3	1.00	102.8	97.7	109.3	100.0	1.00	100.0	64.3	135.6	100.0	1.00	53.1	53.1	53.1
Ulna	42.9	2.33	34.3	8.1	61.4	70.0	1.18	20.1	15.9	32.3	100.0	1.00	119.3	114.2	125.5	66.7	1.00	98.6	46.5	163.6	33.3	1.50	41.5	15.5	62.4
Metacarpal	100.0	1.00	19.9	17.5	21.5	-	-	-	-	-	-	-	-	-	-	66.7	1.20	154.2	142.5	177.9	-	-	-	-	-
Pelvis	61.8	1.01	80.7	21.8	102.0	77.5	1.18	22.5	9.5	38.3	72.1	1.15	82.8	36.7	103.6	66.7	1.20	111.7	23.5	165.3	100.0	1.00	54.8	44.1	65.4
Femur	35.0	1.88	62.8	9.3	85.0	68.8	1.23	24.5	6.9	40.7	47.7	1.69	97.2	18.2	127.3	70.0	1.25	88.4	25.5	165.4	100.0	1.00	62.4	49.4	68.6
Patella	100.0	1.00	14.4	12.8	16.3	100.0	1.00	7.4	7.4	7.4	100.0	1.00	10.4	10.4	10.4	100.0	1.00	8.6	8.6	8.6	-	-	-	-	-
Tibia	58.3	1.50	60.5	4.4	83.0	71.1	1.25	39.3	8.2	50.6	56.3	1.42	107.2	43.9	144.4	46.7	1.88	91.2	37.3	162.5	66.7	1.00	68.9	53.8	76.5
Calcaneus	100.0	1.00	17.7	16.0	19.4	100.0	1.00	10.5	9.4	11.6	87.5	1.00	30.6	29.6	31.9	100.0	1.00	28.7	27.4	29.9	100.0	1.00	22.5	22.5	22.5
Astragalus	100.0	1.00	11.0	9.5	13.8	100.0	1.00	6.5	5.8	7.2	100.0	1.00	20.8	20.0	21.3	100.0	1.00	27.0	18.5	35.6	-	-	-	-	-
Metatarsals	85.7	1.00	9.1	5.5	11.1	100.0	1.00	14.5	13.3	14.8	86.0	1.09	28.5	9.1	48.5	100.0	1.00	159.6	151.1	180.1	-	-	-	-	-
Phalanx 1/2	67.9	1.27	7.7	4.0	9.9	100.0	1.00	7.3	6.6	7.1	90.7	1.00	9.4	4.0	11.2	100.0	1.00	22.3	18.4	29.1	-	-	-	-	-
Phalanx 3	100.0	1.00	5.2	5.2	5.2	100.0	1.00	6.0	5.6	6.1	100.0	1.00	5.4	2.3	6.1	-	-	-	-	-	-	-	-	-	-
Total/Avg	52.4	1.21	30.1	10.4	43.8	47.7	1.30	17.3	7.2	31.5	64.2	1.24	44.6	25.8	57.1	53.5	1.38	74.4	47.1	101.7	79.2	1.04	44.7	34.0	53.5

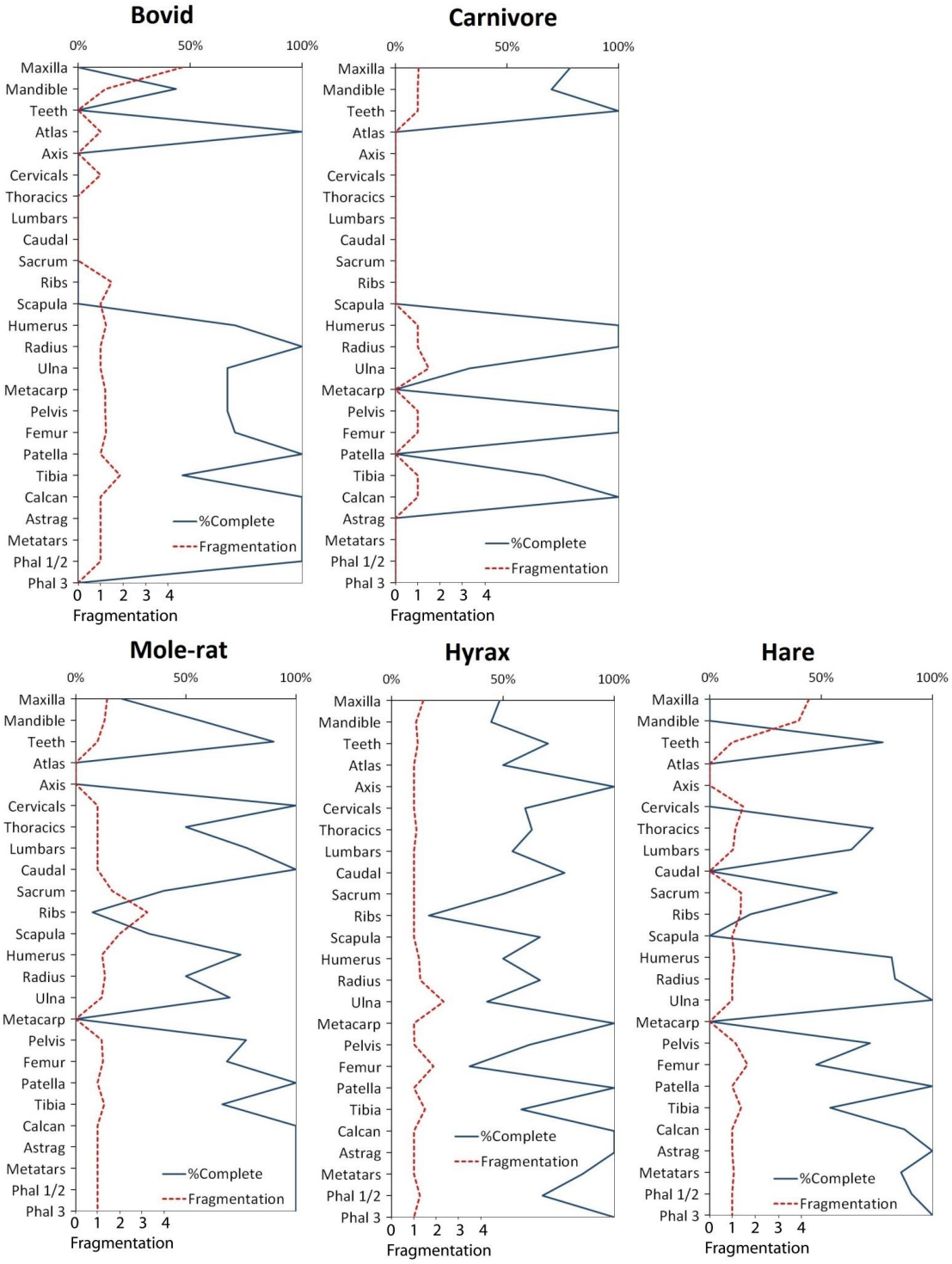


Figure 6. Completeness of bones (percent whole bones) = blue lines, and bone fragmentation ratio (NISP/MNE) = red lines for the prey aggregates

in the Verreaux's Eagle assemblage.

Table 7. Analysis of deviance (Type II tests): results of binomial regression analyses. Df = degrees of freedom; LR Chi-sq = likelihood ratio chi-square; bold values are significant at the 0.05 level.

Effect	Category	*Df*	LR Chi-sq	*P*
Fragmentation	Taxa	4	10.61	**0.03**
	Bone	24	765.97	**<0.01**
Punctures	Taxa	4	12.365	**0.02**
	Bone	42	256.149	**<0.01**
Crenulated edges	Taxa	4	40.510	**<0.01**
	Bone	42	380.340	**<0.01**
Fractured edge	Taxa	4	49.460	**<0.01**
	Bone	42	394.660	**<0.01**
Digestion	Taxa	4	2.461	0.65
	Bone	42	56.073	0.07
Pits	Taxa	4	7.060	0.13
	Bone	42	57.484	0.06
Scores	Taxa	4	3.638	0.46
	Bone	42	59.991	0.35
Notches	Taxa	4	4.336	0.36
	Bone	42	9.785	0.94

hierarchical cluster analysis to compare fragmented to whole bones by skeletal element. The results indicate that there are three patterns of whole bone preservation among the prey groups (Figure 7). Mole-rats and carnivores constitute one cluster and hyraxes compose a second, closely-related cluster exhibiting comparable proportions of whole bone preservation across skeletal elements. This pattern differs from the whole-bone preservation of hares and bovids which are similar to one another and constitute a third cluster. Our principal components analysis (Table 3) supports the cluster analysis as PC1 has the largest loadings for mole-rats, and carnivores and includes the similarly-

fragmented hyraxes. These taxa are approximately equal and they explain 77.8% of the variation in the data. The PC2 explains almost all of the remaining variation and loads for hares and bovids.

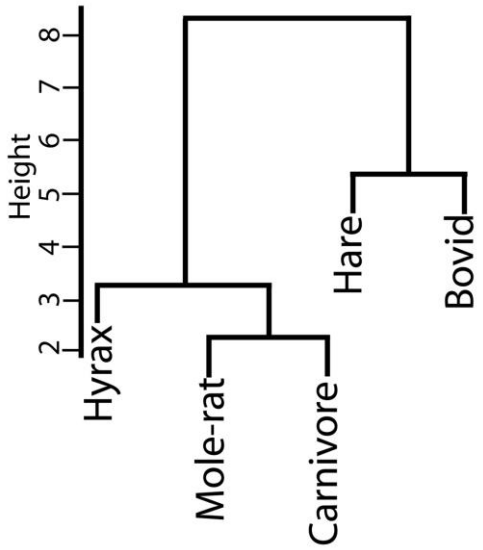


Figure 7. Cluster dendrogram summarizing the ratio of fragmented to whole bones by skeletal element of the mammals recovered from the Verreaux's eagle nests.

4.4 - Bone surface modifications

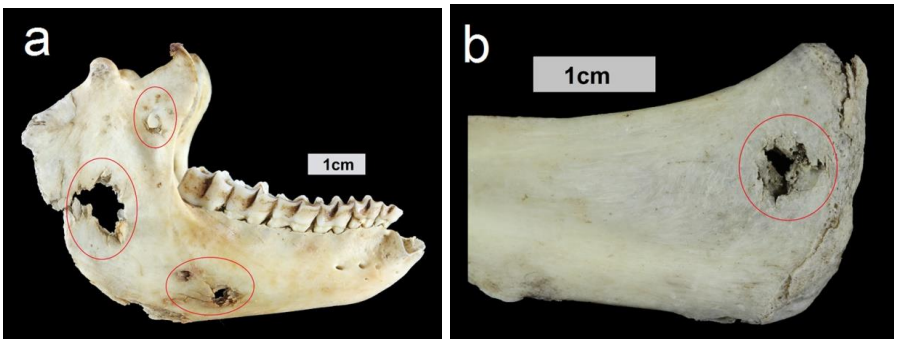
The combined total of surface-modified bone for mammals is 36.9% of NISP (Table 8). (See Appendix B for the frequency of bone surface modifications broken down by skeletal element and taxon.)

4.4.1 - Punctures (Figure 8)

Punctures are the most conspicuous surface modification observed in the assemblage. Most punctures are macroscopic and can be detected with the

naked eye. However, some punctures are extremely small – the smallest is 0.9 mm^2 – and could easily have been missed if not for the use of a microscope. Among the prey aggregates, we observed 276 specimens (9.3% of total NISP) with at least one puncture and 128 specimens had multiple punctures; total number of punctures observed is 460. Carnivore bones (14.8% carnivore NISP) are the most punctured, followed by bovids (13.5% bovid NISP), hyraxes (10.4% hyrax NISP), mole-rats (10.0% mole-rat NISP), and hares (4.5% hare NISP). Punctures almost uniformly occur on specimens with thin cortical bone and underlying trabecular bone, such as crania and mandibles, the epiphyses of long bones and vertebrae. Punctures were not observed on the shafts of long bones and only two occurred on compact bones, a tarsal and a patella.

Cranial bones exhibit the greatest number of specimens with at least one puncture, totaling 138 (15.7% crania NISP). These punctures are more or less evenly distributed across the frontal, parietal, occipital, temporal, and orbital bones; few punctures occur on pre-maxillae and maxillae. Thirty-four mandibles have at least one



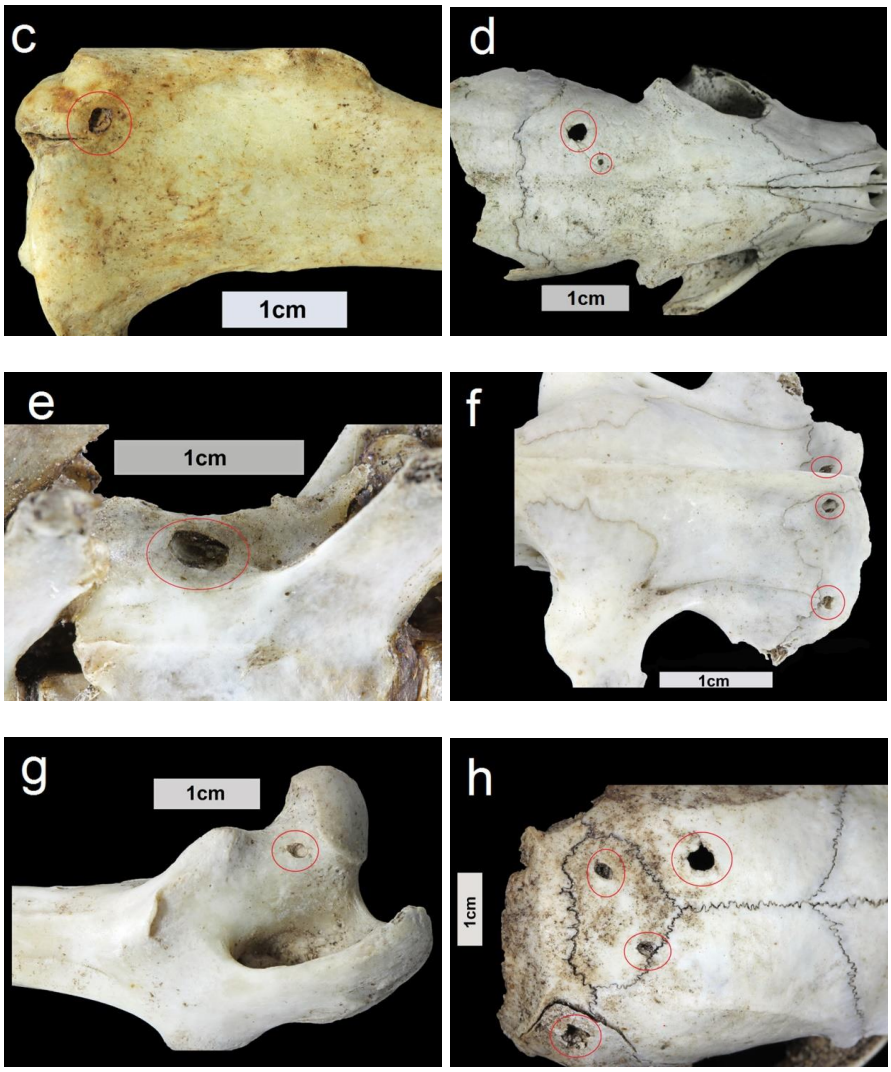


Figure 8. Puncture damage from the Verreaux's eagle sample: (8a) *P. capensis* mandible; (8b) *Lepus* spp. ilium; (8c) *Lepus* spp. proximal tibia; (8d) *G. pulverulenta* cranium; (8e) *Lepus* spp. lumbar vertebrae; (8f) *B. suillus* cranium; (8g) *Lepus* spp. proximal femur; (8h) *P. capensis* cranium.

puncture (5.8% mandible NISP). Most of these appear on the ramus and gonion, while a few are on the coronoid process, mandibular condyle, and mandibular corpus. There are 84 hind limb bones (pelvis, femur, patella, and tibia) that exhibit at least one puncture (14.1% hind limb NISP). Over half– 47 (56.0% hind

limb puncture NISP) – of all hind limb punctures occur on the pelvis; of those 68.5% are located on the ilium. Nineteen femora and 17 tibiae specimens have at least one puncture (12.8% and 10.8% of femora and tibiae NISP). The majority (77.8%) of femoral punctures occur at the distal portion of the bone whereas tibiae punctures mostly (89.5%) occur on the proximal portion. Forelimb (scapula, humerus, radius, and ulna), torso (vertebrae, sacrum, and ribs), and autopodial specimens (carpals, tarsals, metapodia, and phalanges) exhibit the fewest punctures by body part: twelve, four, and four (6.5%, 1.4%, and 1.4% NISP) respectively. Of these elements, only the proximal humerus displays multiple punctures with eight (9.9% humeri NISP).

Table 9 illustrates the shape categories of the observed punctures as well as the location, frequency, minimum, maximum, mean size, and standard deviation of the puncture areas. Oval punctures dominate the assemblage with 58.9% of all punctures, followed by circular (16.1%), irregular (13.7%), triangular (7.2%), and rectangular (4.1%). Irregular punctures are the largest on average (18.5 mm^2) followed by rectangular (15.8 mm^2), oval (13.4 mm^2), circular (7.3 mm^2), and triangular (4.8 mm^2). With the exception of irregular punctures, the different puncture types occur in roughly the same proportions across body portions. Irregular punctures disproportionately occur on cranial specimens (88.9% of all irregular punctures) and most of these are found on the thinnest bones of the cranium (orbits and parietals).

4.4.2 - Pits (Figure 9)

We documented 44 specimens (1.5% of total NISP) with at least one pit; nine specimens exhibited multiple pits, totaling 56 pits. Most pits are small and are difficult to locate without the aid of a microscope and angled light. Carnivore bones (3.7% carnivore NISP) are the most pitted, followed by mole-rats (2.7% mole-rat NISP), bovids (1.9% bovid NISP), hyraxes (1.1% hyrax NISP), and hares (0.7% hare NISP). Unlike the pattern observed with punctured specimens, roughly half (23 pits) of the pits we documented occur on dense cortical bone such as long bone shafts.

Hind limb elements exhibit the greatest number, with at least one pit, totaling 22 (3.7% hind limb NISP). Half of these (10 ilium and one ischium) are found on softer portions of the pelvis. However, seven femora and four tibiae (4.7% and 2.5% femur and tibia NISP) exhibit at least one pit on the cortical portions of bones. Cranial and mandibular bones exhibit the second most pits by body part with 20 (1.4% and 1.4% cranial and mandibular NISP). Cranial pits are located mostly on the frontal and parietal bones; mandibular pits are found mostly on the mandibular corpus under the tooth row. Only two (1.1% forelimb NISP) pits were recorded on bones of the forelimb, both on shaft fragments of proximal humeri. There were no pits found on torso or autopodial specimens.

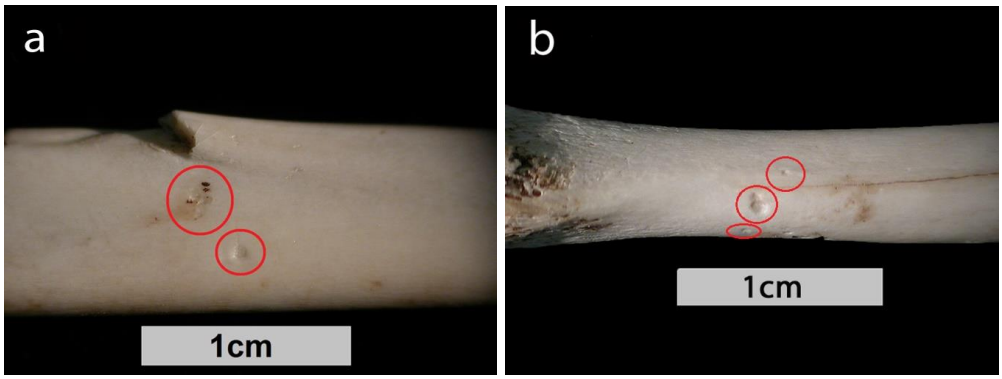


Figure 9. Pit damage from the Verreaux's eagle sample: (9a) *B. suillus* tibia mid shaft; (9b) *Lepus* spp. tibia distal shaft.

4.4.3 - Scores (Figure 10)

There are 41 specimens (1.4% of total NISP) with at least one score. The scores tend to be straight, shallow in depth and U-shaped in cross-section. Most are three to five millimeters in length and do not display a consistent orientation to the bone axis. As with pits, scores are difficult to observe without a microscope. Bovid bones (1.9% bovid NISP) are the most scored, followed by hares (1.8% hare NISP), hyraxes (1.4% hyrax NISP), mole-rats (1.0% mole-rat NISP), and carnivores (0.0% carnivore NISP). There are 27 specimens (66% scored specimens NISP) in which a score and a pit co-occur.

Hind limb elements exhibit the greatest number, with at least one score, totaling 18 (3.0% hind limb NISP). Nine are found on the ilium (3.2% pelves NISP) while two are on the shafts of femora (1.3% femur NISP) and seven are on the tibia shafts (4.4% tibia NISP). Three forelimb elements (1.6% forelimb NISP) have at least one score: one each on the distal scapula, proximal humerus, and

distal radius (2.9%, 1.2%, and 3.6% of each NISP). Four bones of the torso (1.4% torso NISP) show at least one score: three lumbar vertebrae (2.3% lumber NISP) and one sacrum (2.7% sacra NISP). Eight cranial and seven mandibular specimens have scores (0.9% and 1.2% crania and mandible NISP). Only one autopodial bone – an astragalus – is scored (0.4% autopodia NISP).

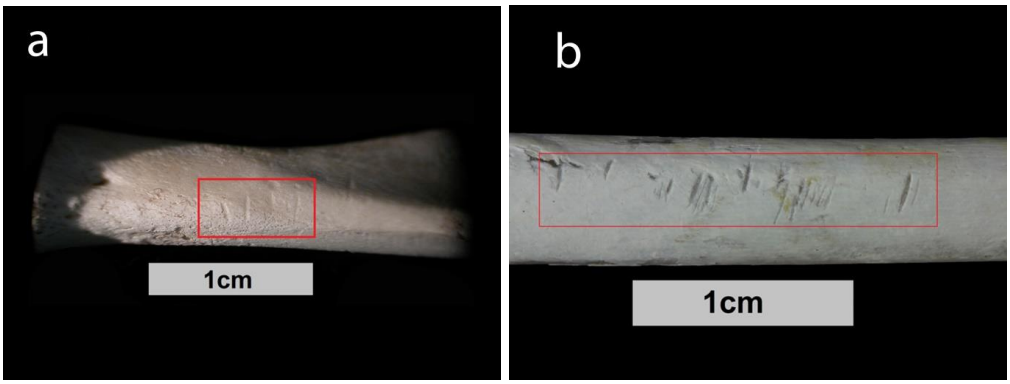


Figure 10. Scores from the Verreaux's eagle sample: (10a) *P. capensis* ilium; (10b) *Lepus* spp. radius mid shaft.

4.4.4 - Notches (Figure 11)

Only two notches were identified in the assemblage (0.1% of total NISP): one is located on the mid-shaft of a bovid femur, the other on the proximal-shaft of a hare tibia. Both are conspicuous and can be observed with the naked eye. Both notches are semicircular as opposed to arcuate-shaped, and the platform angles are oriented perpendicularly; the maximum notch breadths of the bovid femur and hare tibia are nine and six millimeters respectively.

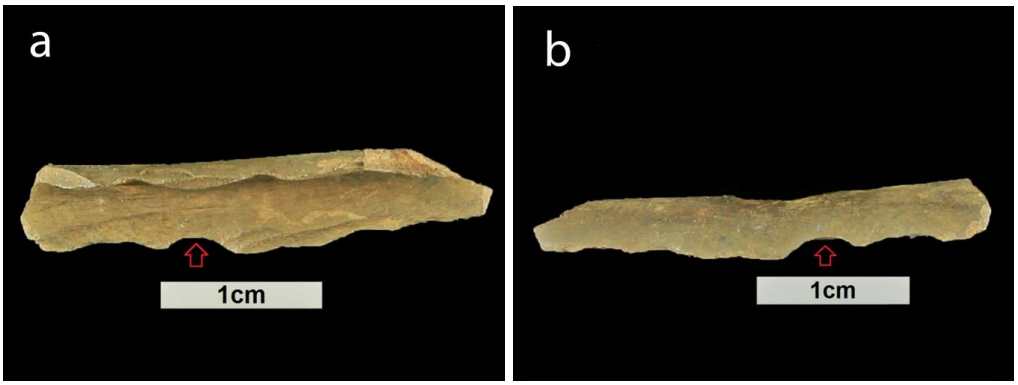


Figure 11. Notch damage from the Verreaux's eagle sample; two views of the same specimen: (11a) *Lepus* spp. tibia shaft, internal view; (11b) *Lepus* spp. tibia shaft, external view.

4.4.5 - Crenulated edges (Figure 12)

A large proportion of the assemblage (261 NISP, 8.8% of total NISP) has crenulated edge damage. The most common area of damage is on the margins of bones, particularly elements that contain thin cortical bone and bone processes, examples include: the spinous and lateral processes of vertebrae, coronoid process of the mandible, and the iliac and ischial bones of the pelvis. Only four long bone specimens – the epiphyses of a humerus, ulna, tibia, and metatarsal – were recorded with crenulated edge damage and there were no small, compact bones that displayed crenulation. This type of damage is macroscopic and can be observed with the naked eye. Carnivore bones (16.7% carnivore NISP) are the most crenulated, followed by hyraxes (11.2% hyrax NISP), mole-rats (7.3% mole-rat NISP), bovids (6.7% bovid NISP), and hares (4.4% hare NISP).

Bones of the torso are the most crenulated (19.9% torso elements NISP): eleven ribs (28.2% rib NISP) exhibit crenulated edge damage, followed by 28 lumbar vertebrae (21.2% lumbar vertebrae NISP), seven sacra (18.9% sacrum NISP), eight thoracic vertebrae (18.2% thoracic vertebrae NISP), and three cervical vertebrae (17.6% cervical vertebrae NISP). Forelimb elements are the second most crenulated (9.7% forelimb elements NISP): 16 scapulae (45.7% scapulae NISP) exhibit crenulated edges, followed by one ulna (2.4% ulnae NISP), and one humerus (1.2% humeri NISP). Cranial and mandibular specimens have 135 examples with crenulation (12.2% mandibles and 7.2% of crania NISP). Fifty hind limb bones (8.4% hind limb elements NISP) are crenulated: 49 pelvis specimens (17.4% pelvis elements NISP) and one tibia (0.6% tibiae NISP). Lastly, one autopodial bone, a proximal metapodial (0.4% autopodial NISP), is crenulated.

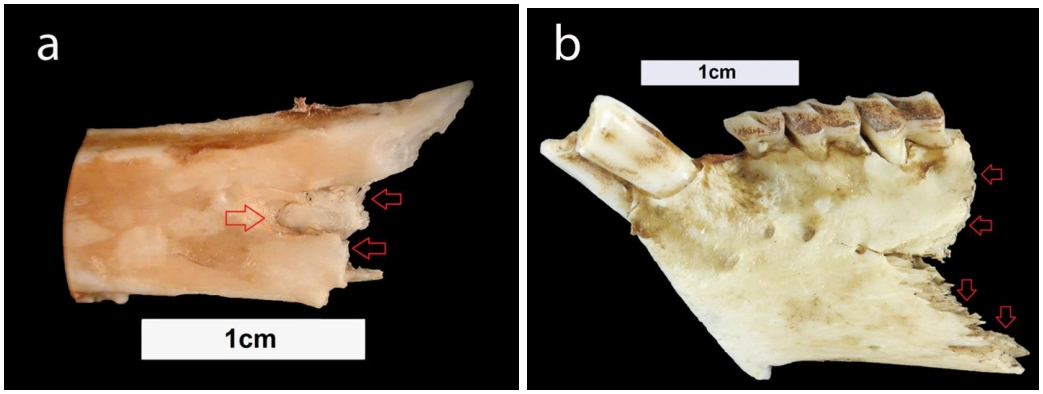


Figure 12. Crenulated edge damage from the Verreaux's eagle sample: (12a) *B. suillus* tibia proximal shaft; (12b) *P. capensis* mandible; (12c) *P. capensis* distal femur (12d) *Lepus* spp. ilium.

4.4.6 - Fractured edges (Figure 13)

Fractured edge damage is the most common bone modification in the assemblage, affecting 15.2% of all specimens by NISP. Skeletal elements with dense cortical bone – such as long bones – exhibit fracture damage more frequently than elements comprised of thin cortical and trabecular bone by a ratio of 2.5 to 1. Fractured edge damage was observed throughout the assemblage on a variety of skeletal elements. Bovid bones (32.7% bovid NISP) are the most fractured, followed by hares (16.5% hare NISP), hyraxes (15.4% hyrax NISP), carnivores (14.8% NISP), and mole-rats (11.1% mole-rat NISP).

Seventy one forelimb elements (38.2% forelimb element NISP) have fractured edges: 39 humeri (48.1% humeri NISP), followed by 19 ulnae (45.2% ulnae NISP), nine radii (32.1% radii NISP), and four scapulae (11.4% scapulae NISP). Hind limb elements are the second most fractured (33.8% hind limb elements NISP): 89 femora are fractured (59.7% femora NISP), followed by 80

tibiae (50.6% tibiae NISP), and four metatarsals (44.4% metatarsals NISP). There are 145 fractured cranial and mandibular specimens (9.1% cranial and mandibular specimens NISP). Nineteen torso specimens exhibit fractures (6.6% torso specimens NISP): eight thoracic vertebrae (18.2 % thoracic vertebrae NISP), two cervical vertebrae (11.8% cervical vertebrae NISP), and nine lumbar vertebrae (6.8% lumbar vertebrae NISP). Lastly, nine autopodial bones are fractured (3.2% autopodia NISP), all are metatarsals (12.0% metatarsals NISP).

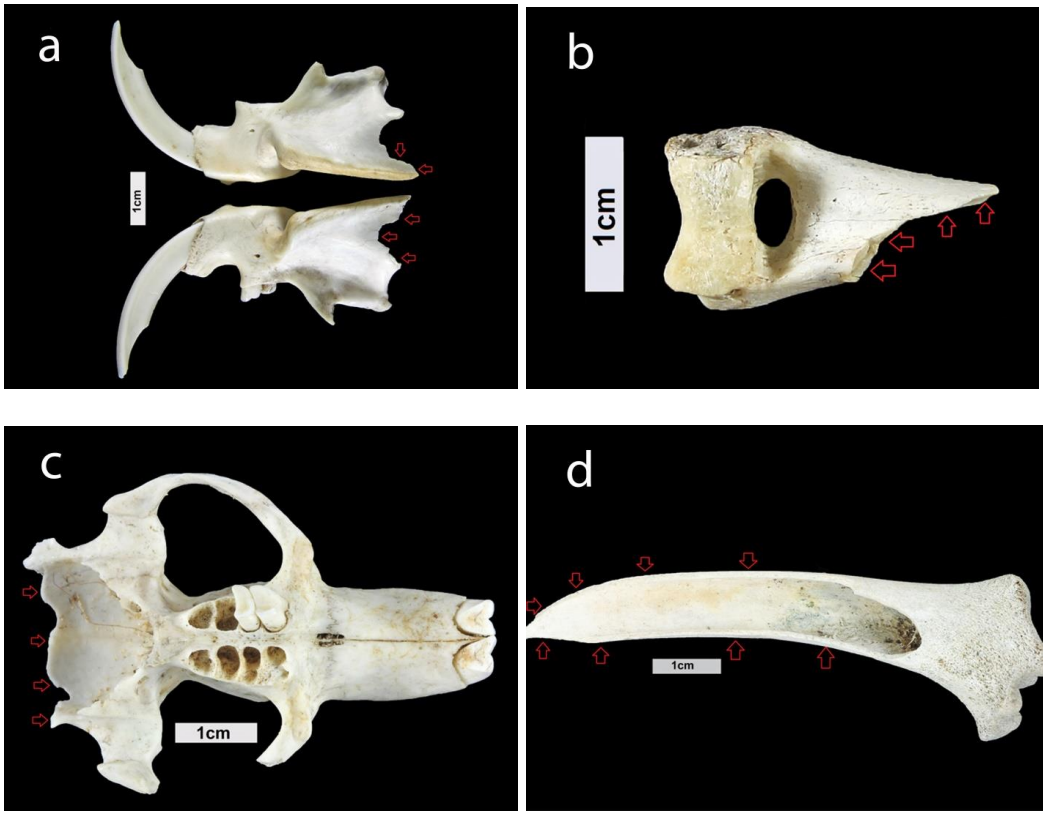


Figure 13. Fractured edge damage from the Verreaux's eagle sample: (13a) *B. suillus* paired mandibles; (13b) *P. capensis* distal humerus; (13c) *B. suillus* cranium; (13d) Size I bovid (juvenile) distal femur shaft.

4.4.7 - Digestion (Figure 14)

Seventeen identifiable bones and two dental specimens (19 total, 0.6% of total NISP) have digestion damage. Fourteen of these specimens were recovered from the five pellets collected under the nests. In addition to the identifiable specimens, the pellets contained many small but unidentifiable bone fragments. All but seven of these fragments were less than two millimeters in maximum dimension; these seven larger fragments did not have identifiable features and were not assigned to element or taxon. Bovid specimens (1.0% bovid NISP) are the most digested followed by mole-rats (0.8% mole-rat NISP), hyraxes (0.6% hyrax NISP), hares (0.5% hare NISP), and carnivores (0.0% carnivore NISP). While digested specimens could be identified macroscopically, studying them with a microscope aided our ability to assess the extent to which the entire specimen was affected and to observe subtle aspects of digestion – such as rounding and localized pitting. For all digested specimens, the entire bone surface was affected and approximately 50% of the bone was destroyed. Twelve bone and the two dental specimens were graded (Table 1) as “3/heavy” digestion and five bone specimens were graded as “4/extreme” digestion. There were no bones assigned to the lesser two categories “1/light” and “2/moderate.”

Eight bones of the torso (2.4% torso NISP) with digestion damage, seven vertebrae and one rib. Three forelimb elements (1.6% forelimb NISP) are digested: one distal humerus, a proximal ulna, and a distal radius. Four cranial specimens and two isolated teeth are digested (0.4% crania NISP). There is one

digested autopodial specimen (0.4% autopodial NISP), a first phalanx from a juvenile bovid. Two hind limb elements (0.3% hind limb NISP) are digested, a mole-rat pelvis and patella.

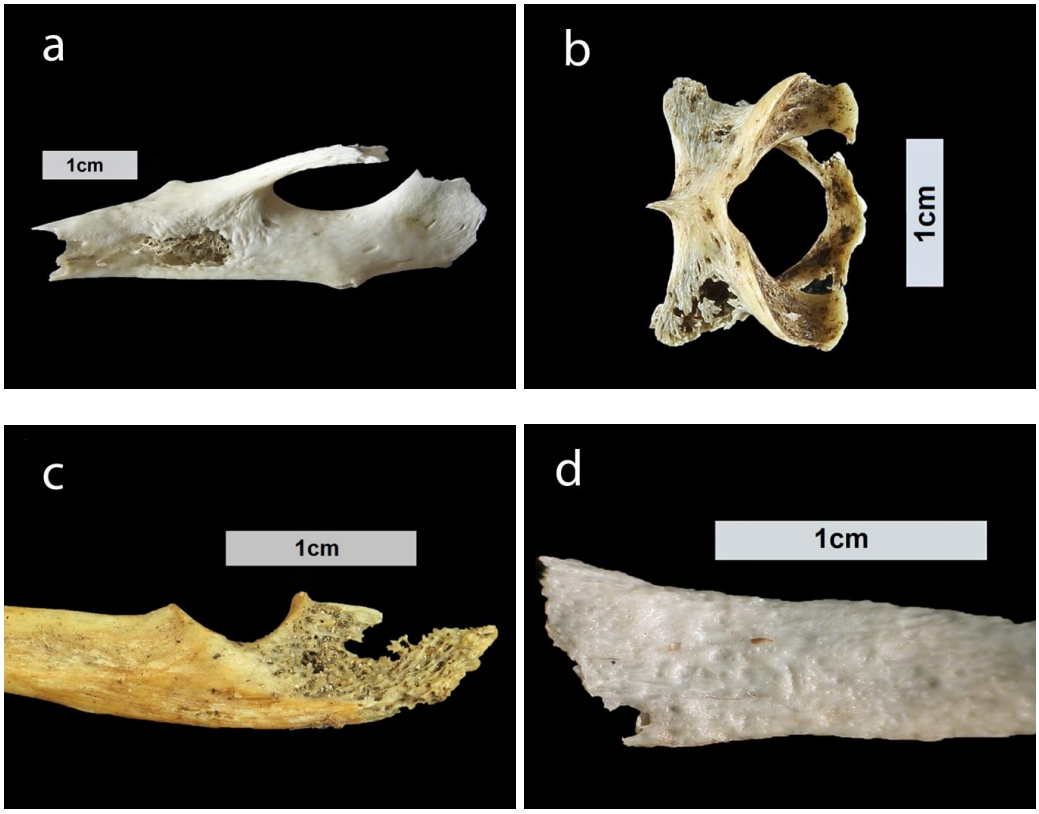


Figure 14. Digestion damage from the Verreaux's eagle sample: (14a) *P. capensis* innominate; (14b) *P. capensis* first cervical vertebrae; (14c) *B. suillus* proximal ulna; (14d) *B. suillus* distal radius shaft.

4.4.8 – Surface modification differences between prey aggregates

There are surface modification frequency differences between the prey aggregates. Figure 15 shows the relative proportion of surface modifications, where the horizontal bars are proportional to the surface modifications as

represented by taxon. Based on Figure 15 and the previous descriptions, there appears to be little proportional difference between the frequencies of pits, scores, notches, and digestion, whereas punctures, crenulated, and fractured edge specimens exhibit frequency variability between prey aggregates. To test whether these observations are significant, we performed a binomial logistic regression analysis (Table 7), providing tests for differences between taxa adjusted for skeletal elements and skeletal elements adjusted for taxa (Type II tests). In our analyses, the differences between both taxa and skeletal elements were not significant for pits, scores, notches, and digestion. That is, the frequencies and locations of these modifications do not vary in significant ways.

Table 8. Frequencies and total bone surface modifications by body part of the mammal prey aggregates for the Verreaux's eagle assemblages.

	(%) Puncture	Pit	Score	Digested	Notch	Crenulated edge	Fractured edge	Total
Hyrax								
Crania	108 (10.8)	5 (0.5)	10 (1.0)	3 (0.3)	0 (0.0)	79 (7.9)	100 (10.0)	305 (30.6)
Torso	0 (0.0)	0 (0.0)	1 (1.0)	4 (3.9)	0 (0.0)	36 (35.3)	12 (11.8)	53 (52.0)
Forelimb	5 (6.7)	0 (0.0)	0 (0.0)	1 (1.3)	0 (0.0)	15 (20.0)	36 (48.0)	57 (76.0)
Hindlimb	43 (17.0)	12 (4.7)	9 (3.6)	1 (0.4)	0 (0.0)	37 (14.6)	80 (31.6)	182 (71.9)
Autopodia	0 (0.0)	0 (0.0)	1 (1.6)	0 (0.0)	0 (0.0)	0 (0.0)	2 (3.2)	3 (4.8)
Total	156 (10.4)	17 (1.1)	21 (1.4)	9 (0.6)	0 (0.0)	167 (11.2)	230 (15.4)	600 (40.1)
Mole-rat								
Crania	50 (10.6)	13 (2.8)	4 (0.8)	1 (0.2)	0 (0.0)	40 (8.5)	34 (7.2)	142 (30.1)
Torso	1 (2.9)	0 (0.0)	0 (0.0)	2 (5.9)	0 (0.0)	3 (8.8)	0 (0.0)	6 (17.6)
Forelimb	3 (5.6)	2 (3.7)	1 (1.9)	2 (3.7)	0 (0.0)	2 (3.7)	17 (31.5)	27 (50.0)
Hindlimb	16 (13.6)	4 (3.4)	2 (1.7)	1 (0.8)	0 (0.0)	7 (5.9)	28 (23.7)	58 (49.2)
Autopodia	1 (3.4)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (3.4)
Total	71 (10.0)	19 (2.7)	7 (1.0)	6 (0.8)	0 (0.0)	52 (7.3)	79 (11.1)	234 (33.0)
Carnivore								
Crania	6 (17.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	8 (22.9)	2 (5.7)	16 (45.7)
Torso	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Forelimb	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	3 (37.5)	3 (37.5)
Hindlimb	2 (25.0)	2 (25.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (12.5)	3 (37.5)	8 (100.0)
Autopodia	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	8 (14.8)	2 (3.7)	0 (0.0)	0 (0.0)	0 (0.0)	9 (16.7)	8 (14.8)	27 (50.0)
Hare								
Crania	4 (6.1)	1 (1.5)	1 (1.5)	2 (3.0)	0 (0.0)	4 (6.1)	5 (7.6)	17 (25.8)
Torso	3 (2.1)	0 (0.0)	3 (2.1)	1 (0.7)	0 (0.0)	18 (12.4)	7 (4.8)	32 (22.1)
Forelimb	3 (9.1)	0 (0.0)	2 (6.1)	0 (0.0)	0 (0.0)	0 (0.0)	4 (12.1)	9 (27.3)
Hindlimb	16 (8.7)	3 (1.6)	5 (2.7)	0 (0.0)	1 (0.5)	4 (2.2)	75 (40.8)	104 (56.5)
Autopodia	1 (0.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	7 (4.3)	8 (4.9)
Total	27 (4.5)	4 (0.7)	11 (1.8)	3 (0.5)	1 (0.2)	26 (4.4)	98 (16.5)	107 (28.6)
Bovid								
Crania	4 (13.3)	1 (3.3)	0 (0.0)	0 (0.0)	0 (0.0)	4 (13.3)	4 (13.3)	13 (43.3)
Torso	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Forelimb	1 (6.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (6.3)	11 (68.8)	13 (81.3)
Hindlimb	7 (21.9)	1 (3.1)	2 (6.3)	0 (0.0)	1 (3.1)	1 (3.1)	15 (46.9)	27 (84.4)
Autopodia	2 (11.1)	0 (0.0)	0 (0.0)	1 (5.6)	0 (0.0)	1 (5.6)	4 (22.2)	8 (44.4)
Total	14 (13.5)	2 (1.9)	2 (1.9)	1 (1.0)	1 (1.0)	7 (6.7)	34 (32.7)	61 (58.7)
Grand total	276 (9.3)	44 (1.5)	41 (1.4)	19 (0.6)	2 (0.1)	261 (8.8)	449 (15.2)	1092 (36.9)

Crania=crania, mandible, teeth; Torso=vertebrae, ribs, sacrum; Forelimb=scapula, humerus, radius, ulna; Hind limb=pelvis, femur, patella, tibia; Autopodial=carpals, tarsals, metapodials, phalanges.

Differences at the 0.05 level for both taxa and skeletal elements were observed for punctures (*Df*=4, *P*=0.02 and *Df*=42, *P*=<0.01), crenulated (*Df*=4, *P*=<0.01 and *Df*=42, *P*=<0.01), and fractured (*Df*=4, *P*=<0.01 and *Df*=42, *P*=<0.01) specimens. These results indicate that there are significant frequency and location differences for punctured, crenulated, and fractured edge specimens among both taxa and skeletal elements.

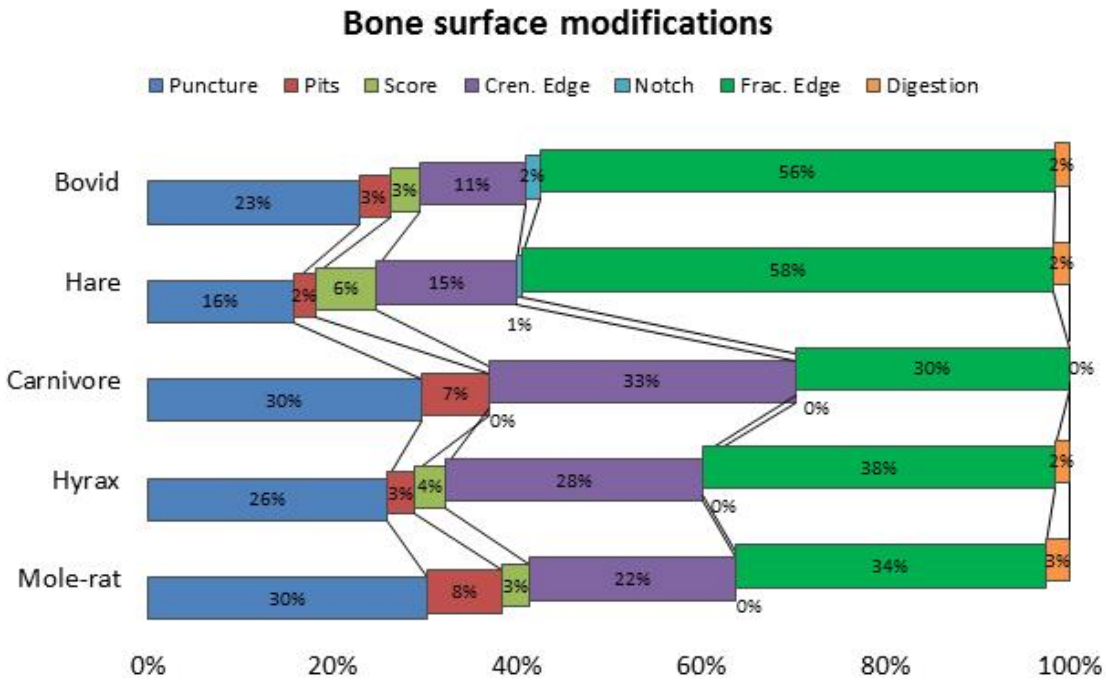


Figure 15. The relative proportions of bone surface modification in the Verreaux's eagle samples by prey aggregate. The horizontal bars are proportional to the surface modifications represented by taxon.

5 – DISCUSSION

5.1 - Prey composition

Rock hyraxes: The fraction of hyrax individuals in our assemblage (45.8% MNI) is less than the MNI reported by Boshoff et al. (1991) acquired from eight VE nests in the Cape Floral Region (60.5% MNI) but is typical of proportions reported in other studies (Hockey et al., 2005). Boshoff et al (1991) showed that local and regional variation could be influenced by the effects on prey availability of topography. Our age profile is similar to the larger sample (from a range of habitats) of hyrax mandibles from VE nests reported by Cruz-Uribe and Klein (1998): 207 (7%) neonates, 355 (12%) juveniles, 682 (23%) subadults, and 1717 (58%) adults. Cruz-Uribe and Klein observed that neonates are less abundant in the VE assemblages than expected based on their representation in live populations whereas the other age-classes are roughly proportional. They reasoned that, according to Davis (1994), neonates remain closer to rocky shelters to avoid predation as VE are unable to obtain individuals who are situated close to the rock face given their predation strategy of approaching at high speed and requiring sufficient space to maneuver. However, seasonal and preservation factors are likely to also contribute to this pattern. Though VE show a preference for hyraxes – accounting for 90% of all prey in some studies

(Gargett, 1990) – they do not show preferences for hyraxes of a particular sex or age-class beyond the scarcity of accumulated neonates.

Table 9. Puncture shape categories, location, frequency, minimum, maximum, mean size, and standard deviation for all prey aggregates from the Verreaux's Eagle assemblages.

Puncture type		N (%)	Cranial	Torso	Fore-limb	Hind limb	Auto-podial	Min. mm²	Max. mm²	Mean mm²	Stand. dev.
Circular		74 (16.1)	39 (52.7)	0 (0.0)	2 (2.7)	32 (43.2)	1 (1.4)	0.85	62.60	7.25	10.11
Irregular		63 (13.7)	56 (88.9)	0 (0.0)	1 (1.6)	6 (9.5)	0 (0.0)	1.60	58.16	18.48	14.75
Oval		271 (58.9)	202 (74.5)	3 (1.1)	10 (3.7)	55 (20.3)	1 (0.4)	1.11	101.28	13.40	16.53
Rectangular		19 (4.1)	11 (57.9)	0 (0.0)	0 (0.0)	7 (36.8)	1 (5.3)	2.58	53.79	15.79	14.24
Triangular		33 (7.2)	19 (57.6)	1 (3.0)	1 (3.0)	11 (33.3)	1 (3.0)	0.86	19.21	4.84	3.96
Total		460	327 (71.0)	4 (0.9)	14 (3.0)	111 (24.1)	4 (0.9)	-	-	-	-

Cape dune mole-rats: Mole-rats are common prey of VE (Hockey et al., 2005). They are represented by a greater fraction in our sample (MNI=25.7%) than the results Boshoff et al. (1991) reported (MNI=12.3%). However, as in their results, adults heavily dominate our sample. The adult-dominated age profile is probably not the result of VE prey choice; it is more likely that the underrepresentation of neonates and juveniles reflects the life-history pattern of mole-rats as the neonate and juvenile age cohorts remain cloistered in their natal burrows and are inaccessible to avian predators until adulthood (Bennett and Faulkes, 2000).

Hares: Hares are frequent prey of VE across multiple regions (Boshoff et al., 1991; Gargett, 1990; Hockey et al., 2005) and represent 8.8% (MNI) of our

sample. For comparison, leporids were 10.7% (MNI) in the Boshoff et al. (1991) prey assemblage. Adults heavily dominate our assemblage, effectively mirroring the results of Cruz-Uribe and Klein (1998) and approximating Hockett's (1991, 1995) humeri fusion data for leporids accumulated by Golden eagles (*Aquila chrysaetos*). There are some differences; the VE assemblages exhibit greater frequencies of fused tibia in relation to the Golden eagle assemblages. The difference may simply be the result of sample size or could reflect differences in predation strategies and/or the ecologies of the hares themselves. Whatever the case, it appears that VE tend to accumulate mature hares. Boshoff et al. reported only 5% juvenile hares in their assemblage. It is possible that VE are deleting young hares from the assemblage by swallowing bones whole and destroying the bones during digestion. But this seems unlikely as the long bones of Cape and especially scrub hare are large and, unlike owls, eagles tend to swallow the bones of their prey less frequently, preferring instead to dismember and swallow boneless portions of their prey (Andrews, 1990; Avery, 1990).

Bovids: We identified at least two species of bovid and together they represent 3.3% (MNI) of our sample. Boshoff et al. (1991) identified five species and, as a whole, bovids contributed a larger portion of their assemblage, 9.4% (MNI). Boshoff et al. used dental eruption where applicable but only report bovid "juveniles" and "adults." However, the criterion used by Boshoff et al. for aging bovid mandibles was comparable to ours (Avery pers. comm.). The two data

sets are similar in revealing that adult bovids are rare in VE assemblages; the number of “adults” reported by Boshoff et al. is 10 individuals (17.5% of bovids).

Carnivores: Boshoff et al. (1991) identified seven species of small carnivores as compared to our three. Carnivores account for 3.3% (MNI) of our sample compared to 6.3% (MNI) in Boshoff et al.’s sample. Like Boshoff et al., we found only adult carnivores in our sample.

The age profiles of prey documented here, and reported elsewhere indicate that VE typically accumulate adult mammals, with the exception of bovids where sub-adult individuals are more common. In this study as well as in others where the sex of the prey has been determined, there does not seem to be a preference for males or females among the taxa. The differences between the proportions of prey represented in our sample and the numbers reported by Boshoff et al. (1991) likely reflect local and sample size differences as their sample consisted of eight nests to our five and included more individuals, an MNI of 608 to our 371. On the whole, the differences are not substantial and we do not think they represent significantly different patterns of predation.

5.2 - Skeletal-Part Representation

The bone relative abundance profiles of VE prey are distinctive. Hyrax, mole-rat, and carnivore prey remains are dominated by cranial and mandibular specimens and, to a lesser extent, hind limb elements. Of notable exception to this pattern is the abundance of hyrax pelves which is the most abundant

postcranial element among the prey cluster. However, the abundance of hyrax pelves is minimized by the lack of all other postcrania, squarely placing the hyraxes with mole-rats and carnivores. The hare and bovid profiles noticeably deviate from hyraxes, mole-rats, and carnivores, exhibiting fewer cranial and mandibular specimens and greater frequencies of postcranial elements, particularly axial and fore limb bones. Our cluster and principal components analyses indicate that the differences in the skeletal-parts profile reflect two discrete patterns, one that characterizes hyrax, mole-rat, and carnivore bone survivorship (even when accounting for the relatively high frequency of hyrax pelves), and another that characterizes hare and bovid bones.

An alternative interpretation is that the skeletal-parts profiles represent three patterns, with hyraxes, mole-rats, and carnivores exhibiting similar skeletal-parts profiles and constituting one cluster, while hares, which might be expected to cluster with the hyraxes, mole-rats, and carnivores due to their similarities in size and body plan, exhibit a different pattern, driven by the near-complete lack of cranial remains. A third pattern, for bovids, is expected as their differences in size and body plan result in different skeletal-parts patterning characterized by a dearth of cranial elements and higher numbers of postcrania.

The dominance of cranial elements among the hyraxes, mole-rats, and carnivores conforms to published accounts of VE feeding behavior (Davis, 1994; Gargett, 1990) and skeletal-parts representation (Brain, 1981; Cruz-Uribe and

Klein, 1998) as does the dominance of postcranial remains among the hares (Cruz-Uribe and Klein, 1998). Additionally, the generally low survivorship of postcranial elements for most prey taxa accords with the feeding habits of VE. Gargett (1990) notes that hunting pairs often partially dismember and consume prey before returning to the nest; presumably some prey body parts are left at such expedient consumption sites. Scavenging and caching of body parts is another behavior (Steyn, 1982) that could influence skeletal-part abundance, particularly in larger prey as, owing to their shape and weight, VE may only transport selected portions of a larger carcass to their nest site. This may explain why there are few bovid cranial remains. Contrariwise, the near absence of hare cranial elements cannot reasonably be attributed to size as hyrax cranial elements are similar in size but in great abundance. The absence of hare crania is likely due to the pneumatized character of the lagomorph skull and mandible (Wible, 2007). This lack of robustness probably results in the more thorough deletion of cranial elements during dismemberment and digestion. As for smaller and broken postcranial elements, these are sometimes swallowed whole by eagles, many of which are subsequently digested completely (Avery, 1990; Andrews, 1990; Boshoff et al. 1990; Lloveras et al. 2008a). It is also possible that some small bones and bone fragments were missed in the collection process. Predictably, fragile and smaller elements such as metapodials, carpals, tarsals, phalanges, and vertebrae are less-well represented.

Our analyses of specimen size and bone structural density indicate that in all but one case – carnivores – individual size instead of structural density is positively and significantly correlated with bone survivorship. Only hares exhibit a positive and significant relationship between survivorship and bone density, a result that mirrors the hare bone density and element representation at VE nests reported by Cruz-Uribe and Klein (1998). VE tend to preserve larger bones and delete small ones regardless of bone density. Again, this preservation pattern probably reflects the eagles' feeding and carcass transport behavior where small, compact skeletal elements are swallowed and destroyed during digestion and larger, meaty bones are transported back to the nest where the bones are stripped of flesh and subsequently discarded.

5.3 - Bone fragmentation and breakage

There are more broken bones in the VE sample than has typically been reported in other eagle prey assemblages (see Appendix C). There are also distinctive patterns of whole bone preservation among the prey aggregates, further suggesting that VE consume individual prey taxa differently. Our logistic regression analysis indicates that fragmentation differences among both taxa and skeletal elements are significantly different. Further, our cluster and principal components analyses demonstrate that mole-rats, carnivores, and hyraxes again exhibit similar proportions of whole bone preservation and that this pattern differs

from the whole-bone preservation of hares and bovids which are more analogous to one another.

Our analysis of long bone fractures found that bone fracturing likely occurred during prey capture and consumption rather than through post-discard breakage. The mammal bones from the VE sample closely match the 'green' breakage patterns of the Fontbrégoua assemblage, whereas they differ considerably from the Sarrians assemblage, in which breakage took place after the bones had dried.

5.4 - Bone surface modifications

Some eagle taxa like the African Crowned eagle (*Stephanoaetus coronatus*) have been described as "fastidious eaters that inflict little damage to bone" (Sanders et al., 2003). This is clearly not the case for VE. We observed bone surface modifications on roughly one-third of the mammal prey remains. Like bone breakage, surface modifications are more common in the VE sample compared to other eagle prey assemblages (see Appendix C). Our detection of bone surface modifications was enhanced by the use of a microscope, notably in relation to small punctures, pits, scores, and digestion. It is possible that where low modification frequencies have been reported the aid of a microscope could result in increased detection of bone modifications. However, given the frequency of modifications that are clearly visible with the naked eye , such as large punctures, crenulated and fractured edges (the three most abundant

surface modifications), we feel the number of modifications observed reflects the behavior of VE in relation to prey capture and consumption as opposed to the lack of detection in other eagle prey assemblages.

The majority of bone surface modifications appear to have been caused by the beaks or talons of VE during capture and/or consumption. There is no evidence of post-discard ravaging by other organisms, though it is possible that scavengers removed some discarded bones from below the nests and feeding perches. However, Steyn (1982) noted that scavengers tend to avoid foraging below active raptor nests lest they become prey.

Modifications in the form of notches and digested bone were seldom observed. The lack of notches may be due to the fact that VE do not regularly exploit within-bone nutrients as do terrestrial carnivores and humans. The scarcity of digested bone reflects the fact that fewer pellets were recovered than expected, implying that VE swallow few bones and/or tend to regurgitate pellets at places other than nest sites and nearby feeding perches. Moreover, the pellets that were recovered contained many small unidentifiable bone fragments, which indicates that when bones are swallowed they are often destroyed. As has been documented with other species of eagle (Andrews, 1991; Avery, 1990), the aggressive digestion of eagles may simply be deleting many of the bones that are swallowed.

There are significant differences in surface modification between the prey aggregates. Our binomial logistic repression analyses indicate that there are frequency differences for puncture, crenulated, and fractured specimens among the taxa and skeletal elements. There are no differences for pits, scores, notches, and digestion. Figure 15 shows the relative proportions of modified bone by prey aggregate; it appears that surface modification differences follow a pattern in which hares and bovids display similar proportions of crenulated and fractured specimens and display the two lowest puncture totals by proportion, whereas hyraxes, mole-rats, and carnivores display greater proportions of punctured and crenulated bone but reduced ratios of fractured specimens in relation to hares and bovids. The surface modification patterns offer further confirmation that VE modify and differentially accumulate the bones of their prey in distinctive ways.

5.5 - VE and other small prey accumulators

One of the primary goals of taphonomy is to determine the agents responsible for the accumulation of a fossil assemblage. To achieve this, distinctive bone surface modifications, breakage patterns, and skeletal-part representation of potential accumulating agents must be identified. To date, much work has been done to distinguish the taphonomic signatures of human and carnivore-accumulated small prey assemblages (Andrews and Evans 1983; Cochard, 2004; 2008; Hockett, 1999; Hockett and Haws, 2002; Lloveras et al.,

2008a; 2011; Lupo and Schmitt, 2002; Mondini, 2004; Munro and Bar-Oz, 2005; Rodríguez-Hidalgo et al, 2013; Schmitt and Juell, 1994; Tagliacozzo and Fiore, 1998; Thompson and Henshilwood, 2014; Yellen, 1991a; 1991b). On the whole, assemblages accumulated by raptors have different taphonomic signatures (Andrews, 1990; Avery, 1990; Bochenski et al., 2009; Hockett, 1991; 1996; Hoffman, 1988; Lloveras et al., 2008b; 2009; Sampson, 2000; Sanders et al., 2003; Trapani et al., 2006) than those accumulated by humans and carnivores. And, among raptors, there are taphonomic differences between diurnal and nocturnal taxa (Andrews, 1990; Avery, 1990; Hockett, 1991; 1996; Lloveras et al., 2008b; 2009), as well as intra-group differences (as documented in this paper).

Appendix C provides small prey skeletal-part preservation, fragmentation, puncture, and digestion comparisons between diurnal and nocturnal raptors and carnivores. In relation to other diurnal raptors, VE contribute conspicuously more damage to the bones of their prey in the form of fragmentation and punctures (usually the only surface modifications, other than digestion, reported in raptor taphonomic studies). They are similar to other diurnal raptors in that cranial and hind limb elements are usually the highest-surviving bones among surface and pellet samples. However, in comparison to nocturnal raptors, VE (and diurnal raptors generally) fragment the bones of their prey far less, resulting in the greater preservation of whole bones. And, though nocturnal raptors tend to swallow and digest prey bones more frequently, VE leave considerably more

puncture marks. Skeletal-part preservation patterns between nocturnal raptors and VE (and diurnal raptors generally) are markedly different in that axial, forelimb, and distal-limb elements are better preserved in nocturnal raptor accumulations. Carnivores and VE appear to fragment and puncture the bones of their prey in similar proportions. However, fewer whole bones are preserved in the carnivore assemblages as they often masticate, swallow, and digest the bones of small prey. The patterns of skeletal-part preservation between carnivores and VE are similar in that hind limb elements are usually better represented; they differ in that axial, forelimb, and distal limb elements are better represented in the carnivore assemblages.

6 – Conclusions

VE are powerful predators capable of killing and lifting animals beyond their own body weight. They also scavenge from carcasses of prey they could not possibly lift whole. Where their prey accumulations have been quantified, it is apparent that VE are prodigious hunters of small mammals, often specializing on hyraxes. It also appears that there is a correlation between local availability of mammalian prey and prey selectivity by these eagles as the proportion of hyraxes in the diet fluctuates between 40-90% and is variously complemented with other locally-available mammals. Based on our study and those of others, hares, mole-rats, bovids, and small carnivores – in addition to hyraxes –

comprise the major component of VE diet in the Cape Floral Region. The recovery of multiple skeletal elements from 19 taxa suggests that the variety of prey in our sample adequately represents the range of prey of VE in the Cape Floral region.

Based on the nature and frequency of bone modifications we have observed, it appears that VE inflict more damage to the bones of their mammalian prey than do other eagle species. Broken and punctured specimens are common bone surface modifications observed in our VE sample, whereas these appear to be less common among other eagle prey accumulations. The frequency of damage inflicted by VE indicates that there is taphonomic variability in the ways that different eagle taxa process their prey and, thereby the accumulations of their prey; there is no “one size fits all” modification pattern for eagles. Taphonomic patterns derived from predation by other eagle taxa do not, therefore, offer the best or appropriate general proxies from which to identify VE predation.

In VE there is patterned variability in the ways they accumulate and modify their prey. There are two distinct skeletal-parts preservation, bone breakage, and bone surface modification patterns among our prey aggregates: one that largely characterizes hyraxes, mole-rats, and carnivores, and another that characterizes hares and bovids. Faunal analysts investigating the potential role of VE at fossil sites should be aware of these taphonomic patterns and

differences and that there is no singular pattern of accumulation, especially in regard to skeletal-part preservation. Nevertheless, there are patterns of preservation, breakage, and bone modification that can be employed on a taxon-specific basis to separate VE prey remains from those of other bone accumulators.

PROLOGUE (Papers 1 & 2)

Paper 2 is the logical next step from paper 1. In the first paper, an analysis of an actualistic/naturally accrued assemblage of prey remains accumulated by Verreaux's eagle, I suggest that taphonomic patterns derived from predation by other eagle taxa are not the most appropriate means to identify Verreaux's eagle predation in faunal assemblages. Documenting and defining the signatures of Verreaux's eagle predation was crucial to this dissertation as Verreaux's eagles often roost in and around rock shelters and caves – locations that attract other bone accumulators, including humans – and are considered a potential contribution to Stone Age fossil sites.

Paper 1 defines the patterns of preservation, breakage, and bone modification that can be employed on a taxon-specific basis to distinguish Verreaux's eagle prey remains from other bone accumulators and demonstrates that there is patterned variability in the ways that Verreaux's eagles accumulate and modify the bones of their prey. Specifically, paper 1 describes two distinct skeletal-parts preservation, bone breakage, and bone surface modification patterns: one that characterizes hyraxes, mole-rats, and carnivores, and another that characterizes hares and bovids.

Paper 2 uses the same methods as in paper 1 but applies them to experimental assemblages created under controlled conditions; included are the prey remains of a coyote, bald eagle, and great horned owl. Distinguishing

between the bones accumulated by different agents such as diurnal raptors, owls, carnivores, and humans is essential to gaining an understanding of human subsistence activity. However, there is a lack of diverse predator and prey experimental, actualistic, and ethnoarchaeological studies such as those that have been essential in establishing the taphonomic criteria underpinning the study of large mammal fossil remains.

Therefore it was necessary to create and assess the small mammal assemblages described in paper 2. These assemblages represent prey accumulations of a diverse range of predators as well as prey of different size and build. Paper 1 clearly indicates differentiations in skeletal-parts representation, surface modifications, and patterns of bone breakage in relation to the type of prey. This observation informed and guided the decision to feed rabbits as well as guinea pigs to the range of predators.

By extending the range of small mammal taphonomic studies to include prey of underrepresented size and morphology, paper 2 elucidates the taphonomic differences between accumulations of small prey of different sizes recovered from the non-ingested and ingested prey remains of a variety of typical accumulators and better develops the diagnostic features that can be used to identify small mammal accumulators in archaeological bone accumulations.

PAPER 2

Eagles, Owls, and Coyotes (Oh My!): Taphonomic analysis of rabbits and guinea pigs fed to captive raptors and coyotes

SUMMARY

There is the potential for multiple accumulating agents of small mammals (<4.5 kg body weight) at fossil sites, however, the lack of diverse predator and prey experimental and actualistic studies often makes it difficult to attribute the accumulator(s) of small mammals. I report the results of experimentally created assemblages of rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) fed to a bald eagle (*Haliaeetus leucocephalus*), great horned owl (*Bubo virginianus*), and coyote (*Canis latrans*). The analysis provides a taphonomic assessment of two small mammal taxa that differ in size and build and are broadly representative of small mammals recovered from archaeological sites. The digested and undigested portions of the prey remains were analyzed for skeletal-, digested-, deleted-, and fractured-part representation, bone breakage, and bone surface modifications. The rabbit and guinea pig samples are compared and taphonomic differences between predators and prey taxa are observed. The predators produced variable and distinctive intra- and interspecific skeletal-, digested-, deleted-, and fractured-part profiles. Bone surface modification frequency differences between the samples show a mixture

of significant and non-significant intra- and interspecific comparisons. This study expands the range of small mammal experimental and actualistic studies to include prey of underrepresented size and build (guinea pigs) and characterizes the signatures of predator accumulations of small mammals. Often archaeological assemblages feature a mixture of accumulators, this analysis of raptor and carnivore predation on rabbits and guinea pigs will aid in the differentiation of predation between raptors, carnivores, and humans in the archaeological record.

1. INTRODUCTION

In recent years the role of small prey in human subsistence strategies has received considerable attention, particularly in relation to the increase in dietary breadth around the Middle and Upper Paleolithic transition in Eurasia (Cochard et al., 2012; Fa et al., 2013; Lloveras et al., 2011; Stiner, 2009; 2013; Stiner et al., 2000; Tortosa et al., 2002) and modern human origins research in Africa (Clark and Kandel, 2013; Dusseldorp, 2010; 2012; Thompson, 2010; Steele and Klein, 2009). In addition to dietary breadth, the study of small prey has the potential to inform us about paleodemography (Stiner, 2001; 2004; Stiner et al., 1999; 2000), population mobility and landscape use (Hockett and Haws, 2002; Langejans et al., 2012; Stiner et al., 1999; Thompson and Henshilwood, 2014), division of labor (Bird et al., 2005), site occupation intensity (Hockett and Haws,

2002; Lupo and Schmitt, 2005; Rodríguez-Hidalgo et al, 2013a; Stiner, 2013), socioeconomic status (Schmitt and Lupo, 2008), environmental and economic stress (Langejans et al., 2012; Lupo, 2007; Stiner, 2004, 2013; Stiner and Munro, 2011), technological complexity (Backwell et al., 2008; Hockett and Bicho, 2000; Jones, 2006; Steele and Klein, 2009; Wadley, 2010), and the experimentation and transition to domesticatable resources (Munro, 2004a; 2004b). However, the attribution of small prey accumulations are especially challenging as there is potential for multiple accumulating agents: anthropogenic, intrusive, mammalian carnivore, and/or raptor derived (Lloveras et al, 2010). The taphonomic hurdle for faunal analysts rests in distinguishing between these possible bone accumulation origins in order to correctly attribute the fossil accumulator(s).

Central to the challenge of interpreting small mammal (mammals <4.5 kg adult body weight) assemblages is taphonomic attribution. There is the lack of diverse predator and prey experimental, actualistic, and ethnoarchaeological studies such as those that have been essential in establishing the taphonomic criteria underpinning the study of large mammal fossil remains. However, small mammal taphonomy has been strong in two areas: the predator acquisition and bone modification of (1) leporids (Álvarez et al., 2012; Armstrong and Avery, 2014; Avery, 1990; Cochard, 2004a; 2004b; 2008; Cruz-Uribe and Klein, 1998; Hockett, 1991; 1995; 1996; Lloveras et al., 2008a; 2008b; 2009; 2010; 2012a; 2012b; 2014; Pavoa and Stahl, 1999; Rodríguez-Hidalgo et al., 2013b; Sanchis Serra, 2000; Schmitt, 1995; Schmitt and Juell, 1994) and (2) primates (McGraw

et al., 2006; Mitani et al., 2001; Pobiner et al., 2007; Sanders et al., 2003; Tappen and Wrangham, 2000; Trapani et al., 2006) by raptors and mammals. The leporid studies have been instrumental in the interpretation of faunal assemblages and forager life-ways around the Mediterranean basin (Bicho et al., 2000; Cochard et al., 2012; Fa et al., 2013; Hockett and Bicho, 2000; Hockett and Haws, 2002; 2009; Munro, 2009; Stiner and Munro, 2011; Stiner et al., 1999; 2000), while studies of primate remains have been critical in establishing the role of raptors and mammalian carnivores in the accumulation of hominin and primate fossils (Berger and Clarke, 1995; 1996; Gilbert et al., 2009; Hedenström, 1995; McGraw and Berger, 2013).

Collectively, these and other studies (Andrews, 1990; Andrews and Evans, 1983; Elkin and Mondini, 2001; Erlandson et al., 2007; Hockett, 1999; Landt, 2007; Lupo and Schmitt, 2002; 2005; Mondini, 2004; Munro and Bar-Oz, 2005; Schmitt and Lupo, 2008; Tagliacozzo and Fiore, 1998; Yellen, 1991a; 1991b, and others) form the core of small mammal comparative taphonomy. Yet the criteria used to characterize the signatures of predator involvement in small mammal accumulations and the range of variability within those signatures remain less-well defined. For instance, some raptor predation studies (Bochenski et al., 2009; Erlandson et al., 2007; Hockett, 1995, 1996; McGraw et al., 2006; Sanders et al., 2003; Schmitt, 1995; Trapani et al., 2006) have documented minimal levels of prey anatomical part patterning and bone surface damage while others (Andrews, 1990; Bochenski et al., 1997; Brain, 1981; Cruz-

Uribe and Klein, 1998; Hoffman, 1988; Lloveras et al., 2008a; Msuya, 1993) have recognized extensive bone modification and patterning.

Small mammal (or prey) is an extraordinarily broad category that groups taxonomically disparate organisms into a single class usually based on size. Stiner and colleagues (2000) discussed the distinct biological properties of small prey, noting that they differ greatly in their morphology and predator avoidance adaptations among other characteristics. Because of these differences, it cannot be assumed that the taphonomic pattern of one small mammal taxon will resemble the pattern of another (Armstrong and Avery, 2014). It stands to reason that leporids and primates are not representative of the variety of small mammal archaeofaunas. In addition to the range in taphonomic variability between different prey taxa, variation is also introduced by the acquisition, transport, and modification tendencies of the particular predator responsible for accumulation. For instance, Andrews (1990) described the different prey skeletal-part and bone surface modification (BSM) patterns of various diurnal and nocturnal raptors as well as differences between specific predator taxa within those broad divisions. The taphonomic variation produced by diverse predators and prey points to the fact that more actualistic and experimental studies are needed, studies that include a wider variety of small mammals and their predators in order to refine the criteria essential to identifying the accumulator(s) of small mammal assemblages.

Towards this objective I describe and compare the taphonomic profiles of experimentally created assemblage of rabbits (*Oryctolagus cuniculus*) and guinea pigs (*Cavia porcellus*) accumulated by a bald eagle (*Haliaeetus leucocephalus*), great horned owl (*Bubo virginianus*), and coyote (*Canis latrans*). Distinguishing between the bones accumulated by different agents and documenting the range of variation inherent to diverse prey is essential to interpreting small mammal faunal assemblages. The predators featured in this study are native to the Western Hemisphere but are representative of the diurnal and nocturnal raptors and small/medium canids that are often responsible for the accumulation of small mammal fossil remains in multiple locales. The guinea pig (GP) is similar in body plan and size to other small mammals that frequently occur in fossil and archaeological assemblages, such as bathyergids, cavids, scuirids, and larger-bodied muroids (among others), of which there are few taphonomic studies. The rabbit is analogous to other leporid taxa that are often recovered at fossil and archaeological sites. The two prey species differ greatly in terms of body plan and size, and comparisons between these experimentally derived assemblages provide a taphonomic assessment of different sized small mammals collected by a variety of predators.

Predators such as eagles, owls, and canids often live and feed in or around locations that attract humans such as rock shelters and caves. It stands to reason that prey remains accumulated by these predators and humans can become interspersed, and it is often these locales which feature archaeological

deposits. Therefore, differentiating between human and predator accumulated prey remains is crucial for interpreting human subsistence behaviors and site formation processes. Towards this end, the taphonomic profiles described and compared for each prey and predator in this study include: skeletal-part representation, bone breakage, and BSMs for ingested, non-ingested, and where possible deleted bone. The aims of this paper are: (1) to extend the range of small mammal taphonomic studies to include prey of underrepresented size and morphology, (2) to elucidate the taphonomic differences between accumulations of small prey of different sizes (rabbits and GPs) recovered from the non-ingested and ingested prey remains of a variety of typical accumulators (eagles, owls and canids), and (3) to better develop the diagnostic features that can be used to identify small mammal accumulators in archaeological bone accumulations.

2. MATERIALS AND METHODS

For this study, 10 adult rabbits and GPs each were fed to a captive bald eagle (BE), great horned owl (GHO), and coyote, totaling 30 rabbit and 30 GPs. The raptors used in this study are housed at the University of Minnesota College of Veterinary Medicine Raptor Center, which specializes in raptor veterinary services and the rehabilitation of injured birds. The coyote is housed at the Carlos Avery Wildlife Science Center of Minnesota, which focuses on wildlife

education, conservation, and rehabilitation of injured animals. Twenty rabbits and all GPs used in this study were purchased from Rodent Pro, a distributor specialized in supplying feeder animals to zoos and institutions that house carnivorous animals. The 10 rabbits that were fed to the coyote were donated by a local farmer who raises meat rabbits. The average weights of the rabbits fed to the BE, GHO, and coyote were: 3.8 kg, 3.5 kg, and 4.0 kg, and for the GPs: 1.3 kg, 1.3 kg, and 1.6 kg respectively.

The study sample comprises six assemblages: (1) BE-rabbit, (2) BE-GP, (3) GHO-rabbit, (4) GHO-GP, (5) coyote-rabbit, and (6) coyote-GP. Each of these assemblages consists of an ingested portion (raptor pellets and coyote scat) and a non-ingested portion that may have been chewed but was not ingested by the predators. In all there were 18 BE-rabbit, 24 BE-GP, 56 GHO-rabbit, and 62 GHO-GP pellets recovered; the majority of pellets contained bone specimens. The coyote samples consisted of 49 and 42 scats containing rabbit and GP bones respectively; the majority of scats contained bone specimens.

2.1. Feeding protocol and sample preparation

Before each feeding episode, the predators' enclosures were cleaned of previous meals, pellets, and scats. Each rabbit and GP was fed individually to a single predator. The predators were allowed to free feed until the carcass was completely consumed or the predator lost interest and ceased feeding on the remains for at least three days. Throughout the feeding phase of the experiment

the raptors were fed only mice and the coyote was fed only boneless meals to avoid contamination of the rabbit and GP scat samples.

For the raptors, feeding typically lasted between three and five days. At the end of each day, the carcass was removed, weighed, and introduced again to the bird the next morning. Over the course of the feedings, the raptors consumed at least 50% of each carcass by weight. After feeding, the enclosures were cleaned of all non-ingested and ingested prey remains – including fur, bones, pellets, and tissues. Over the next five days, all pellets were collected and associated with the previous feeding episode.

The coyote typically consumed the entire animal within fifteen minutes of its introduction to the enclosure. At the end of the day, the coyote enclosure was cleaned of prey remains and scat. Over the next five days, all scats associated with the previous feeding episode were collected. There was a minimum of five days between each feeding episode for each predator. The predators' enclosures are such that they could be monitored at all times, which helped ensure that prey remains were found and collected.

Where necessary, the skin and fur of all non-ingested prey remains were removed and the bones were gently boiled in plain water to detach adhering tissues. Ingested remains were not boiled given their fragile nature. Pellets were disaggregated by hand with the aid of forceps; coyote scats were wet screened through nested sieves (the smallest screen being 2 mm). Prey remains retrieved

from scats were then soaked in a water and ammonia solution for 24 hours to remove harmful parasites and bacteria. The skeletal remains were not handled again until completely dry.

2.2. Skeletal element representation, quantification, and terminology

The portion of preserved bone and the orientation of paired elements (right or left side of the body) was identified and recorded. An attempt was made to identify each specimen regardless of size. Most specimens could be identified to a specific skeletal element, however some fragmentary specimens lacked diagnostic features and were identified as vertebrae fragment, long bone shaft fragment, tooth fragment, and unidentifiable fragment >2 mm. Bone fragments that were unidentifiable and <2 mm in maximum dimension were not quantified. When summed, *NISP* refers to identified skeletal elements, whereas fragmentary specimens that lack diagnostic features but >2mm are referred to as *n*. The maximum length and width of each specimen was measured using digital calipers as were bone punctures. To estimate skeletal-part frequencies, Relative Abundance (RA) of each skeletal element as stated by Andrews (1990) was calculated. Relative bone proportion indices were also calculated after Andrews (1990).

2.3. Fragmentation and breakage

Skeletal element fragmentation was recorded following a method for small mammals described by Lloveras et al. (2008a). This detailed method allows for

comparison of skeletal-part frequencies of similar small mammal accumulations and facilitates aggregation of element categories for comparison with other data sets. Long bone breakage morphology (fracture angle, fracture outline, and fracture edge) was recorded following Villa and Mahieu (1991). Fragmentation indices and whole bone percentages were calculated for each skeletal element by dividing NISP by MNE and whole bones by NISP respectively.

2.4. Surface modifications

All specimens were inspected with a 10-40x binocular zoom microscope under high incident light to examine for and document BSMs. Digestive alteration to teeth and bones was observed and recorded after Andrews (1990) and summarized according to Lloveras et al. (2008a). The characterization, frequency, and location of punctures (Andrews, 1990; Binford, 1981; Blumenschine et al., 1996; Brain, 1981; Elkin and Mondini, 2001; Hockett, 1991, 1995; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al. 2007; Sanders et al., 2003; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014; Trapani et al., 2006), pits (Binford, 1981; Blumenschine and Selvaggio, 1988; Blumenschine et al., 1996; Domínguez-Rodrigo and Piqueras, 2003; Domínguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al. 2007; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014), scores (Binford, 1981; Blumenschine et al., 1996; Bunn, 1981; Elkin and Mondini, 2001; Haynes, 1980;

1982; 1983; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al., 2007; Sanders et al., 2003; Shipman, 1981; Shipman and Rose, 1983; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014; Trapani et al., 2006), notches (Binford, 1981; Blumenschine and Selvaggio, 1991; Brain, 1981; Capaldo and Blumenschine, 1994; Domínguez-Rodrigo et al., 2013; Fisher, 1995; Haynes, 1982; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al., 2007), crenulated (Binford, 1978, 1981; Brain, 1981; Domínguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Fisher, 1995; Lyman, 1994; Pickering and Wallis, 1997; Landt, 2007) and fractured edge (Binford, 1981; Domínguez-Rodrigo et al., 2013; Johnson, 1985; Landt, 2007; Pickering and Wallis, 1997) were recorded using criteria adopted from established sources in the taphonomic literature.

In regards to punctures and pits, the beaks/talons/teeth of predators create these BSMs during prey capture, transport, and consumption. Punctures are characterized as deep indentations that penetrate the bone cortical surface; punctures may breach the bone (especially thin bone) or only the cortical surface where crushed cortical and cancellous bone is visible around the base and margins of the puncture. Pits are characterized as shallow indentations that do not penetrate the entire bone cortical surface and where some crushing of the cortical surface is visible. The recognition of punctures and pits in non-ingested bone is straightforward. However, recognition in ingested samples is more difficult as they can become distorted or eliminated when passed through the

digestive systems of a predator. In addition, gastric etching can produce puncture- and pit-like features that superficially mimicking those produced by beaks/talons/teeth. In this study a cautious approach has been taken towards the recognition of punctures and pits from the ingested samples. To accurately attribute punctures and pits, the extent of digestion damage to the entire specimen is considered; punctures and pits on specimens that are extremely corroded and thinned (Lloveras et al., 2008a) are typically considered the result of digestion. When crushed trabecular and cortical bone is visible at the base and around the margins of the punctures or pits and where digestion damage is moderate or light, these are typically considered beak/talon/tooth derived.

2.5. Bone density

To investigate the role of bone structural density in the survivorship of prey skeletal-parts, we used bone density values of related taxa of similar size and build as estimates are not available for the specific taxa used in this study. *Lepus californicus* (Pavao and Stahl, 1999) bone density values were substituted for rabbits and *Marmota monax* (Lyman et al, 1992) values were used for GPs. These bone estimates were derived by measuring bone density at specific scan sites on the skeleton using photon densitometry. The bone volume density estimates include both the mineral content and the bone volume measured at the scan site. Though performed on different taxa, the methods and calculations used to derive the bone density values are comparable across the density

estimates. Preferably, bone density estimates obtained from computed tomography or photon densitometry that accounts for variation in the shape of bone cross-sections would have been utilized (Lam and Pearson, 2005; Lam et al, 2003). However, the present study is limited by (1) the need to apply density estimates that most accurately represent the taxa in our sample and (2) the methodological necessity of employing density estimates that were obtained with comparable techniques.

2.6. Statistical analysis

Binomial logistic regression analysis (Hosmer et al, 2013) was used with respect to (1) BSMs and (2) digestion due to their dichotomous nature (i.e. two possible values, modified/digested or not). This multivariate procedure permits the discovery of complex relationships between one or more dependent categorical variables (BSM and degree of digestion) and a set of nominally scaled independent variables (predator and/or prey taxa and skeletal elements) and is used to identify independent variables that are significantly associated with the dependent variable. Chi-square tests of independence were used for intra- and interspecific head-to-head comparisons of predator and prey non-ingested-, ingested-, deleted-, and fragmented-parts (non-ingested samples) profiles to determine if the categorical distributions of one sample differ from another. Principal component analyses (Podani, 1994) were conducted utilizing a matrix of BSM profiles and other sample traits to determine if the suite of bone attributes

can be used to differentiate the samples into distinct clusters by prey accumulator. The 'princomp' function of the R statistical software package (version 2.15.3) with default parameters was used. All other statistical analyses were performed with R version 2.15.3.

3. RESULTS

3.1. Skeletal-part representation

A total of 16,450 specimens were analyzed for this study. Table 10 shows the skeletal-part representation of non-ingested, ingested, and deleted specimens as well as the total number of specimens represented in each of the BE, GHO, and coyote samples. Also shown are the minimum number of elements (MNE), percent relative abundance (%RA), and percentage of deleted bones (%Del, bones that are unaccounted for). For comparison, Fig. 16 depicts the percentages of non-ingested, ingested, and deleted bones by skeletal element for the predator samples. All skeletal elements are at least minimally represented in the sample totals and a minimum number of individuals (MNI)

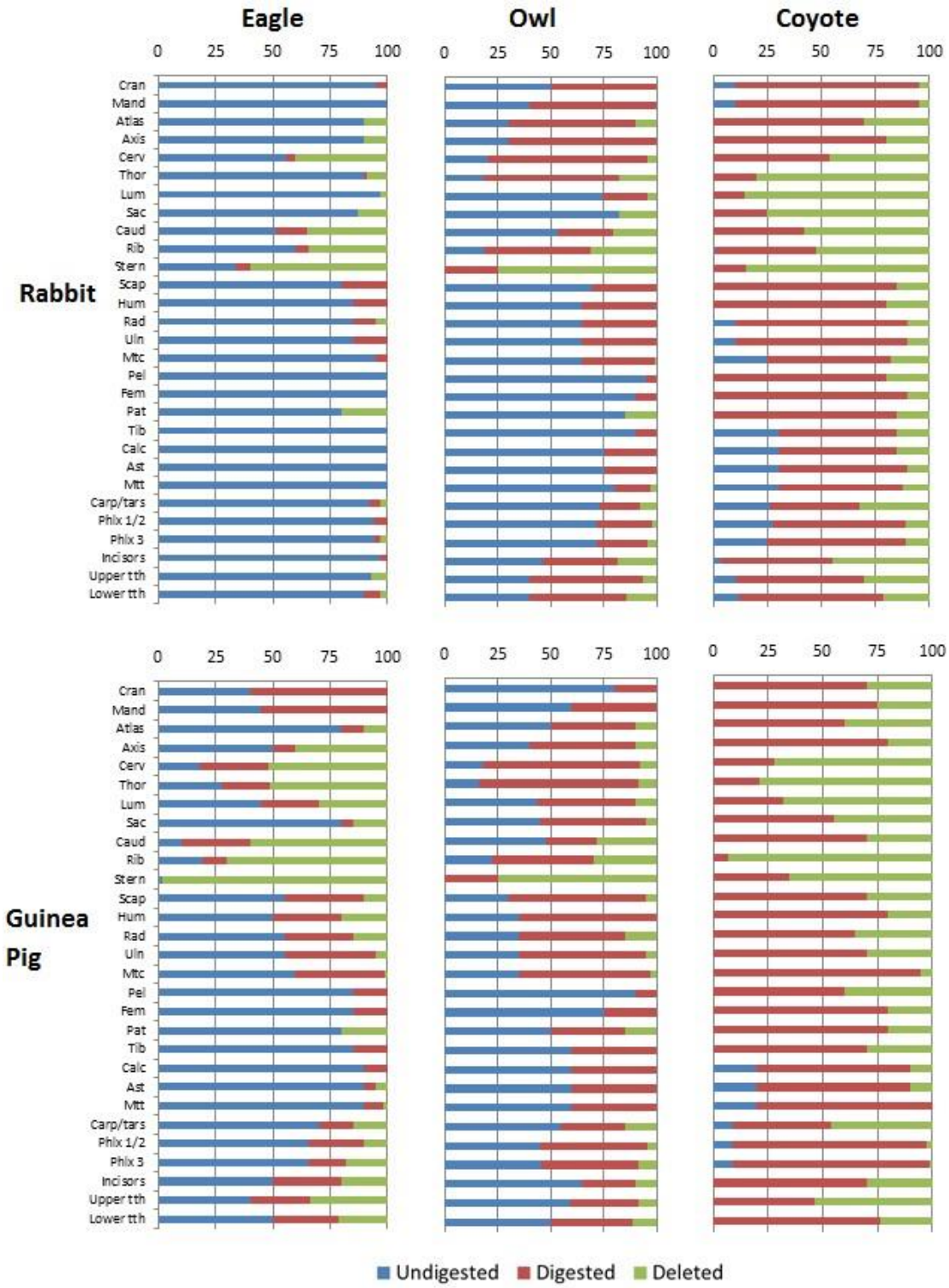


Figure 16: Skeletal part frequencies (%RA, relative abundance) for non-ingested (blue), ingested (red), and deleted (green) skeletal elements for

rabbits and guinea pigs fed to the predators. Numbers on the x-axis are percent.

of 10 was observed for each sample, though the most abundant skeletal element often varied between the samples.

Table 10: Number of specimens (n), minimum number of elements (MNE), percent relative abundance (%RA), and percent deleted bones by relative abundance (%Del) for rabbits and guinea pigs fed to each predator.

Bald Eagle																					
	Rabbit (MNI = 10)											Guinea Pig (MNI = 10)									
	Undigested			Digested			Deleted		Total			Undigested			Digested			Deleted		Total		
	n	MNE	%RA	n	MNE	%RA	MNE	%Del	n	MNE	%RA	n	MNE	%RA	n	MNE	%RA	MNE	%Del	n	MNE	%RA
Cran	35	19	95.0	5	1	5.0	0	0.0	40	20	100	15	8	40.0	17	12	60.0	0	0.0	32	20	100
Man	27	20	100	4	0	0.0	0	0.0	31	20	100	10	9	45.0	14	11	55.0	0	0.0	24	20	100
Atlas	9	9	90.0	0	0	0.0	1	10.0	9	9	90.0	8	8	80.0	2	1	10.0	1	10.0	10	9	90.0
Axis	9	9	90.0	0	0	0.0	1	10.0	9	9	90.0	5	5	50.0	1	1	10.0	4	40.0	6	6	60.0
Cerv	33	28	56.0	5	2	4.0	20	40.0	38	30	60.0	9	9	18.0	17	15	30.0	26	52.0	26	24	48.0
Thor	108	108	90.0	6	1	0.8	11	9.2	114	109	90.8	38	36	27.7	33	27	20.8	67	51.5	71	63	48.5
Lum	68	68	97.1	0	0	0.0	2	2.9	68	68	97.1	27	27	45.0	23	15	25.0	18	30.0	50	42	70.0
Sac	40	35	87.5	0	0	0.0	5	12.5	40	35	87.5	17	16	80.0	1	1	5.0	3	15.0	18	17	85.0
Caud	82	82	51.3	22	22	13.8	56	35.0	104	104	65.0	5	5	10.0	15	15	30.0	30	60.0	20	20	40.0
Rib	191	156	60.0	27	15	5.8	89	34.2	218	171	65.8	62	50	19.2	58	27	10.4	183	70.4	120	77	29.6
Stern	22	20	33.3	4	4	6.7	36	60.0	26	24	40.0	1	1	1.7	0	0	0.0	59	98.3	1	1	1.7
Scap	30	16	80.0	8	4	20.0	0	0.0	38	20	100	19	11	55.0	11	7	35.0	2	10.0	30	18	90.0
Hum	27	17	85.0	5	3	15.0	0	0.0	32	20	100	12	10	50.0	11	6	30.0	4	20.0	23	16	80.0
Rad	17	17	85.0	5	2	10.0	1	5.0	22	19	95.0	13	11	55.0	11	6	30.0	3	15.0	24	17	85.0
Uln	18	17	85.0	4	3	15.0	0	0.0	22	20	100	13	11	55.0	11	8	40.0	1	5.0	24	19	95.0
Mtc	90	90	95.0	12	5	5.0	0	0.0	102	95	100	48	48	60.0	37	31	38.8	1	1.3	85	79	98.8
Pel	20	20	100	1	1	0.0	0	0.0	21	21	100	21	17	85.0	7	3	15.0	0	0.0	28	20	100
Fem	20	20	100	0	0	0.0	0	0.0	20	20	100	20	17	85.0	8	3	15.0	0	0.0	28	20	100
Pat	17	16	80.0	0	0	0.0	4	20.0	17	16	80.0	16	16	80.0	0	0	0.0	4	20.0	16	16	80.0
Tib	23	20	100	0	0	0.0	0	0.0	23	20	100	21	17	85.0	11	3	15.0	0	0.0	32	20	100
Fib	na	na	na	na	na	na	na	na	na	na	na	21	17	85.0	0	0	0.0	3	15.0	21	17	85.0
Calc	20	20	100	0	0	0.0	0	0.0	20	20	100	18	18	90.0	2	2	10.0	0	0.0	20	20	100
Ast	20	20	100	0	0	0.0	0	0.0	20	20	100	18	18	90.0	1	1	5.0	1	5.0	19	19	95.0
Mtt	80	80	100	0	0	0.0	0	0.0	80	80	100	54	54	90.0	7	5	8.3	1	1.7	61	59	98.3
Car/tar	222	222	92.5	11	11	4.6	7	2.9	233	233	97.1	126	126	70.0	27	27	15.0	27	15.0	153	153	85.0
Phlx 1/2	322	322	94.7	21	21	5.3	0	0.0	343	343	100	184	184	65.7	68	68	24.3	28	10.0	252	252	90.0
Phlx 3	170	165	94.4	5	5	2.8	5	2.8	175	170	97.2	92	92	65.7	21	21	16.4	25	17.9	113	113	82.1
Incisors	67	65	96.7	4	2	3.3	0	0.0	71	67	100	22	20	50.0	16	12	30	8	20.0	38	32	80.0
Up tth	115	112	93.3	0	0	0.0	8	6.7	115	112	93.3	32	32	40.0	29	21	26	27	33.7	61	53	66.3
Low tth	90	90	90.0	8	7	7.0	3	3.0	98	97	97.0	40	40	50.0	24	23	29	17	21.2	64	63	78.8
Vert ind	0	-	-	69	-	-	-	-	69	-	-	0	-	-	43	-	-	-	-	43	-	-
LBS	0	-	-	0	-	-	-	-	0	-	-	0	-	-	9	-	-	-	-	9	-	-
>2mm	0	-	-	54	-	-	-	-	54	-	-	0	-	-	128	-	-	-	-	128	-	-
Tth ind	0	-	-	3	-	-	-	-	3	-	-	0	-	-	52	-	-	-	-	52	-	-
Total	1992	1883	-	283	109	-	249	(8.8)	2275	1992	-	987	933	-	715	372	-	543	(21.3)	1702	1305	-

Great Horned Owl

	Rabbit (MNI = 10)											Guinea Pig (MNI = 10)										
	Undigested			Digested			Deleted		Total			Undigested			Digested			Deleted		Total		
	n	MNE	%RA	n	MNE	%RA	MNE	%Del	n	MNE	%RA	n	MNE	%RA	n	MNE	%RA	MNE	%Del	n	MNE	%RA
Cran	24	10	50	80	10	50	0	0	104	20	100	24	16	80	36	4	20	0	0	60	20	100
Man	12	8	40.0	46	12	60.0	0	0.0	58	20	100	16	12	60.0	17	8	40.0	0	0.0	33	20	100
Atlas	3	3	30	10	6	60.0	1	10.0	13	9	90	5	5	50.0	4	4	40.0	1	10.0	9	9	90
Axis	3	3	30.0	7	7	70.0	0	0.0	10	10	100	5	4	40.0	6	5	50.0	1	10.0	11	9	90.0
Cerv	10	10	20.0	43	38	76.0	2	4.0	53	48	96.0	9	9	18.0	47	37	74.0	4	8.0	56	46	92.0
Thor	27	22	18.3	98	77	64.2	21	17.5	125	99	82.5	21	21	16.2	126	98	75.4	11	8.5	147	119	91.5
Lum	54	52	74.3	29	15	21.4	3	4.3	83	67	95.7	30	26	43.3	46	28	46.7	6	10.0	76	54	90.0
Sac	37	33	82.5	0	0	0.0	7	17.5	37	33	82.5	9	9	45.0	10	10	50.0	1	5.0	19	19	95.0
Caud	85	85	53.1	45	42	26.3	33	20.6	130	127	79.4	24	24	48.0	12	12	24.0	14	28.0	36	36	72.0
Rib	65	49	18.8	501	131	50.4	80	30.8	566	180	69.2	61	58	22.3	318	125	48.1	77	29.6	379	183	70.4
Stern	0	0	0.0	15	15	25.0	45	75.0	15	15	25.0	0	0	0.0	16	15	25.0	45	75.0	16	15	25.0
Scap	24	14	70.0	88	6	30.0	0	0.0	112	20	100	13	6	30.0	51	13	65.0	1	5.0	64	19	95.0
Hum	15	13	65.0	14	7	35.0	0	0.0	29	20	100	7	7	35.0	23	13	65.0	0	0.0	30	20	100
Rad	14	13	65.0	12	7	35.0	0	0.0	26	20	100	7	7	35.0	22	10	50.0	3	15.0	29	17	85.0
Uln	14	13	65.0	12	7	35.0	0	0.0	26	20	100	7	7	35.0	19	12	60.0	1	5.0	26	19	95.0
Mtc	65	65	65.0	45	34	34.0	1	1.0	110	99	99	28	28	35.0	55	50	62.5	2	2.5	83	78	97.5
Pel	25	19	95.0	1	1	5.0	0	0.0	26	20	100	19	18	90.0	6	2	10.0	0	0.0	25	20	100
Fem	23	18	90	6	2	10.0	0	0.0	29	20	100	21	15	75.0	13	5	25.0	0	0.0	34	20	100
Pat	17	17	85	0	0	0.0	3	15.0	17	17	85	10	10	50.0	7	7	35.0	3	15.0	17	17	85
Tib	18	18	90.0	5	2	10.0	0	0.0	23	20	100	12	12	60.0	20	8	40.0	0	0.0	32	20	100
Fib	na	na	na	na	na	na	na	na	na	na	na	11	11	55.0	8	6	30.0	3	15.0	19	17	85
Calc	15	15	75.0	5	5	25.0	0	0.0	20	20	100	12	12	60.0	8	8	40.0	0	0.0	20	20	100
Ast	15	15	75	5	5	25.0	0	0.0	20	20	100	12	12	60.0	8	8	40.0	0	0.0	20	20	100
Mtt	64	64	80	20	14	17.5	2	2.5	84	78	98	36	36	60.0	28	25	40.0	0	0.0	64	61	100
Car/tar	162	176	73	49	46	19.2	18	7.5	211	222	93	99	99	55.0	71	71	30.0	27	15.0	170	170	85.0
Phlx 1/2	245	245	72.1	98	87	25.6	8	2.4	343	332	97.6	128	128	45.4	147	142	50.7	11	3.9	275	270	96.1
Phlx 3	133	129	71.7	48	44	24.4	7	3.9	181	173	96	64	64	45.7	64	64	45.7	12	8.6	128	128	91.4
Incisors	28	28	46.7	25	21	35.0	11	18.3	53	49	81.7	26	26	65.0	16	10	25.0	4	10.0	42	36	90.0
Up tth	48	48	40.0	79	64	53	8	6.7	127	112	93.3	49	47	58.8	31	26	33	7	8.7	80	73	85.0
Low tth	40	40	40.0	58	46	46.0	14	14.0	98	86	86.0	40	40	50.0	39	31	39	9	11.2	79	71	98.8
Vert ind	0	-	-	45	-	-	-	-	45	-	-	0	-	-	66	-	-	-	-	66	-	-
LBS	0	-	-	22	-	-	-	-	22	-	-	0	-	-	29	-	-	-	-	29	-	-
>2mm	0	-	-	309	-	-	-	-	309	-	-	0	-	-	485	-	-	-	-	485	-	-
Tth ind	0	-	-	79	-	-	-	-	79	-	-	0	-	-	44	-	-	-	-	44	-	-
Total	1285	1225	-	1899	751	-	264	(8.7)	3184	1976	-	805	769	-	1898	857	-	243	(10.0)	2703	1626	-

Coyote

	Rabbit (MNI = 10)											Guinea Pig (MNI = 10)										
	Undigested			Digested			Deleted		Total			Undigested			Digested			Deleted		Total		
	n	MNE	%RA	n	MNE	%RA	MNE	%Del	n	MNE	%RA	n	MNE	%RA	n	MNE	%RA	MNE	%Del	n	MNE	%RA
Cran	12	2	10.0	140	17	85.0	1	5.0	152	19	95	0	0	0.0	91	14	70.0	6	30.0	91	14	70
Man	4	2	10	93	17	85.0	1	5.0	97	19	95	0	0	0.0	64	15	75.0	5	25.0	64	15	75
Atlas	0	0	0.0	15	7	70.0	3	30.0	15	7	70.0	0	0	0.0	12	6	60.0	4	40.0	12	6	60.0
Axis	0	0	0.0	12	8	80.0	2	20.0	12	8	80.0	0	0	0.0	15	8	80.0	2	20.0	15	8	80.0
Cerv	0	0	0.0	36	27	54.0	23	46.0	36	27	54.0	0	0	0.0	34	14	28.0	36	72.0	34	14	28.0
Thor	0	0	0.0	48	24	20.0	96	80.0	48	24	20.0	0	0	0.0	66	27	20.8	103	79.2	66	27	20.8
Lum	0	0	0.0	51	10	14.3	60	85.7	51	10	14.3	0	0	0.0	86	19	31.7	41	68.3	86	19	31.7
Sac	0	0	0.0	22	10	25.0	30	75.0	22	10	25.0	0	0	0.0	13	11	55.0	9	45.0	13	11	55.0
Caud	11	0	0.0	65	67	41.9	93	58.1	76	67	41.9	0	0	0.0	37	35	70.0	15	30.0	37	35	70.0
Rib	1	1	0.4	298	123	47.3	136	52.3	299	124	47.7	0	0	0.0	97	18	6.9	242	93.1	97	18	6.9
Stern	0	0	0.0	14	9	15.0	51	85.0	14	9	15.0	0	0	0.0	26	21	35.0	39	65.0	26	21	35.0
Scap	0	0	0.0	28	17	85.0	3	15.0	28	17	85	0	0	0.0	36	14	70.0	6	30.0	36	14	70.0
Hum	0	0	0.0	79	16	80.0	4	20.0	79	16	80	0	0	0.0	48	16	80.0	4	20.0	48	16	80.0
Rad	2	2	10.0	38	16	80.0	2	10.0	40	18	90.0	0	0	0.0	26	13	65.0	7	35.0	26	13	65.0
Uln	2	2	10.0	33	16	80.0	2	10.0	35	18	90	0	0	0.0	21	14	70.0	6	30.0	21	14	70.0
Mtc	25	25	25.0	89	57	57.0	18	18.0	114	82	82	0	0	0.0	111	76	95.0	4	5.0	111	76	95.0
Pel	0	0	0	67	16	80.0	4	20.0	67	16	80	0	0	0.0	51	12	60.0	8	40.0	51	12	60
Fem	0	0	0	63	18	90.0	2	10.0	63	18	90	0	0	0.0	52	16	80.0	4	20.0	52	16	80
Pat	0	0	0.0	20	17	85.0	3	15.0	20	17	85.0	0	0	0.0	17	16	80.0	4	20.0	17	16	80.0
Tib	12	6	30	61	11	55.0	3	15.0	73	17	85	0	0	0.0	37	14	70.0	6	30.0	37	14	70
Fib	na	na	na	na	na	na	na	na	na	na	na	0	0	0.0	11	5	25.0	15	75.0	11	5	25.0
Calc	6	6	30	16	11	55.0	3	15.0	22	17	85	4	4	20.0	16	14	70.0	2	10.0	20	18	90
Ast	6	6	30	14	12	60.0	2	10.0	20	18	90	4	4	20.0	15	14	70.0	2	10.0	19	18	90.0
Mtt	24	24	30	85	46	57.5	10	12.5	109	70	88	12	12	20.0	67	48	80.0	0	0.0	79	60	100.0
Car/tar	63	63	26.3	99	99	41.3	78	32.5	162	162	67.5	16	16	8.9	81	81	45.0	83	46.1	97	97	53.9
Phlx 1/2	93	93	27.4	293	210	61.8	37	10.9	386	303	89	24	24	8.6	287	248	88.6	8	2.9	311	272	97.1
Phlx 3	45	45	25.0	115	115	63.9	20	11.1	160	160	88.9	12	12	8.6	138	126	90.0	2	1.4	150	138	98.6
Incisors	2	2	3.3	48	31	52	27	45.0	50	33	55	0	0	0.0	46	28	70	12	30.0	46	28	70.0
Up tth	12	12	10.0	108	72	60.0	36	30.0	120	84	70.0	0	0	0.0	44	37	46	43	53.7	44	37	46.3
Low tth	12	12	12.0	88	67	67.0	21	21.0	100	79	79.0	0	0	0.0	64	61	76	19	23.7	64	61	76.3
Vert ind	0	-	-	125	-	-	-	-	125	-	-	0	-	-	58	-	-	-	-	58	-	-
LBS	0	-	-	156	-	-	-	-	156	-	-	0	-	-	27	-	-	-	-	27	-	-
>2mm	0	-	-	1111	-	-	-	-	1111	-	-	0	-	-	788	-	-	-	-	788	-	-
Tth ind	0	-	-	41	-	-	-	-	41	-	-	0	-	-	29	-	-	-	-	29	-	-
Total	332	303	-	3571	1166	-	771	(29.8)	3903	1469	-	72	72	-	2611	1041	-	737	(35.0)	2683	1113	-

3.1.1. Rabbit ingested-part representation

The coyote ingested the most rabbit bones by both n (3571) and MNE (1166); the BE produced the fewest, n (280) and MNE (109). The relative abundance (Table 10 and Fig. 17) and skeletal element proportion indices (Table 11) demonstrate that:

- The coyote-rabbit ingested sample is dominated by cranial, forelimb, and hind limb elements; axial elements were less-frequently ingested. The coyote's skeletal element proportion indices (Table 11) show that:
  - (PC=C) postcranial and cranial bones were ingested in approximately equal proportions
  - (ZE<ST) lower limb bones were less frequently ingested than upper limb bones
  - (AN=PO) anterior and posterior limb bones were ingested in approximately equal proportions
  - (AX<AP) axial bones were less frequently ingested than appendicular bones
- The great horned owl-rabbit ingested sample is dominated by vertebrae (cervical and thoracic), ribs, and cranial elements and, to lesser extent, forelimb bones; distal limb and lumbar vertebrae were the least-ingested elements. The GHO's skeletal element proportion indices (Table 11) show that:

- (PC<C) postcranial bones were ingested less frequently than cranial bones

Table 11: Relative numbers of digested and deleted skeletal elements comparing proportions of postcranial to cranial elements (PC/C)[a], lower limb to upper limb elements (ZE/ST)[b], anterior to posterior limb elements (AN/PO)[c], and axial to appendicular elements (AX/AP)[d] for rabbits and guinea pigs fed to each predator.

Indices	Eagle		Owl		Coyote	
Digested	Rabbit	GP	Rabbit	GP	Rabbit	GP
PC/C	300.0	39.1	40.9	150.0	100.0	110.3
ZE/ST	83.3	111.1	100.0	105.6	79.4	85.9
AN/PO	1200.0*	250.0	540.4	218.2	104.8	98.3
AX/AP	12.1	77.5	233.3	122.2	56.0	61.9
Deleted	Rabbit	GP	Rabbit	GP	Rabbit	GP
PC/C	-	400.0*	-	-	300.0	72.2
ZE/ST	100.0*	50.0	-	-	83.3	156.3
AN/PO	25.0	250.0	33.3*	166.7	91.7	104.5
AX/AP	338.1	330.9	355.2	147.0	420.9	209.4

[a] Number of femur + humerus / mandibles + maxillae x 100.
[b] Number of tibia + (radius + ulna)/2 / femur + humerus x 100. Radius + ulna divided by 2 to correct for number of elements.
[c] Number of scapula + humerus + (radius + ulna)/2 / pelvis + femur + tibia x 100. Radius + ulna divided by 2 to correct for number of elements.
[d] Number of atlas + axis + (cervical/5) + (thoracic/12) + (lumbar/7) + (sacra/4) / (humerus/2) + (radius/2) + (ulna/2) + (femur/2) + (patella/2) + (tibia/2) x 100. Bones divided by number of times they occur to correct for number of elements.

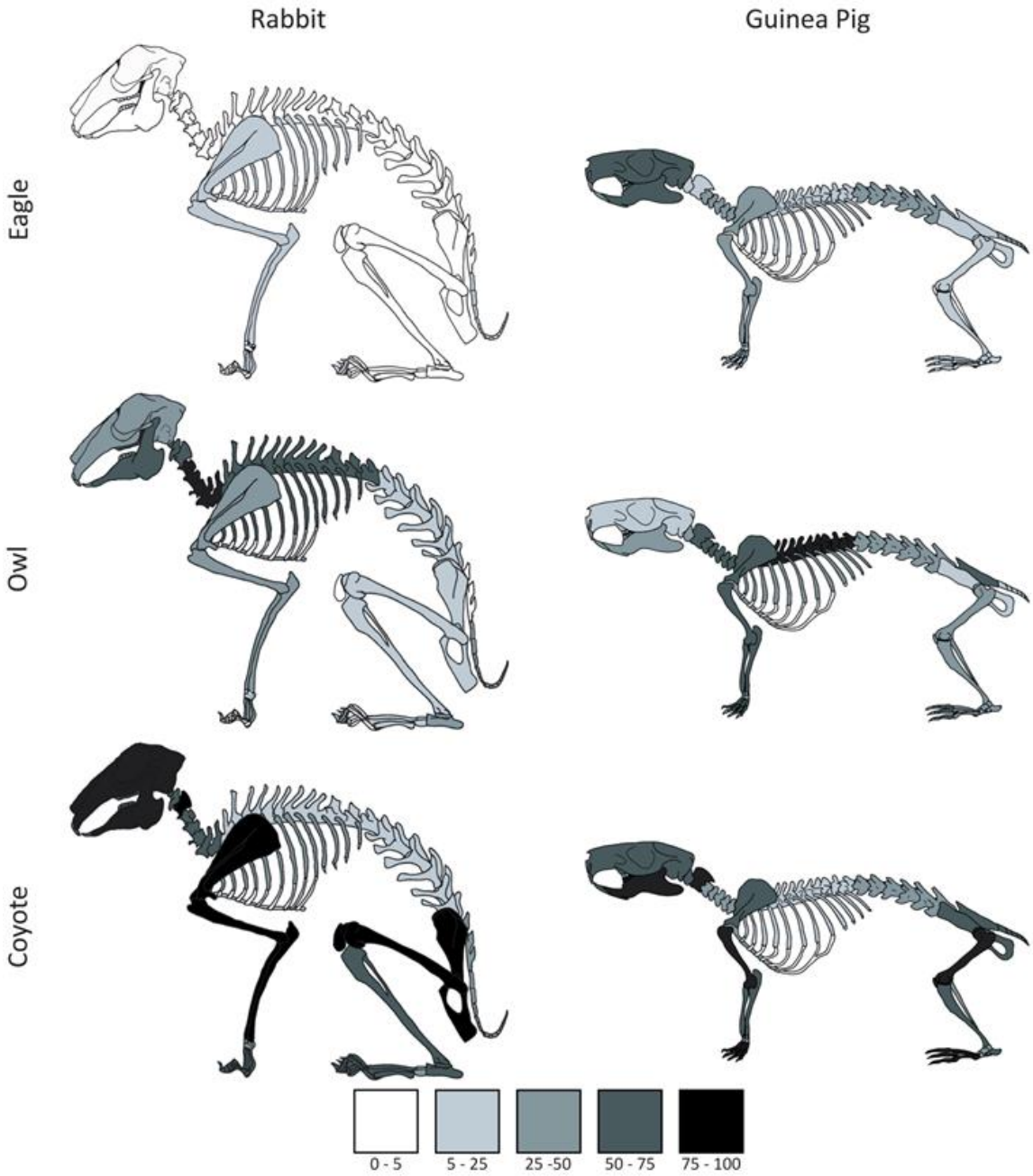


Figure 17: Digested part frequencies (% relative abundance) by skeletal element for rabbits and guinea pigs fed to the predators.

- (ZE=ST) lower and upper limb bones were ingested in equal proportions
- (AN>PO) anterior bones were ingested far more frequently than posterior bones
- (AX>AP) axial bones were ingested far more frequently than appendicular bones

- The comparatively few bald eagle-rabbit ingested bones clustered around the forelimbs, sternebrae, and ribs; cranial, axial, and distal limbs show little digestion damage. The BE's skeletal element proportion indices (Table 11) show that:
  - (PC>C) postcranial bones were more frequently ingested than cranial bones
  - (ZE<ST) there are slightly fewer ingested lower limb bones than upper limb bones
  - (AN>PO) ingested anterior bones greatly outnumber posterior bones
  - (AX<AP) there far fewer ingested axial bones than appendicular bones

3.1.2. Guinea pig ingested-part representation

The coyote ingested the most GP bones by both n (2207) and MNE (1041), more than tripling the totals produced by the BE, n (715) and MNE (372). The relative abundance (Table 10 and Fig. 17) and skeletal element proportion indices (Table 11) demonstrate that:

- The coyote-guinea pig ingested sample is dominated by cranial, forelimb, and hind limb bones; axial bones and ribs were less-frequently ingested. The coyote's skeletal element proportion indices (Table 11) show that:
    - (PC>C) there are slightly more ingested postcranial bones than cranial bones
    - (ZE<ST) lower limb bones were ingested less frequently than upper limb bones
    - (AN=PO) anterior and posterior bones were ingested in about equal proportions
    - (AX<AP) axial bones were ingested less frequently than appendicular bones
- The great horned owl-guinea pig ingested sample is dominated by axial and forelimb bones; crania and pelvis are the least ingested elements. The GHO's skeletal element proportion indices (Table 11) show that:
    - (PC>C) postcranial bones were more frequently ingested than cranial bones
    - (ZE=ST) lower and upper limb bones were ingested in approximately equal proportions
    - (AN>PO) ingested anterior bones greatly outnumber posterior elements
    - (AX>AP) axial bones were ingested slightly more frequently than appendicular bones

- The bald eagle-guinea pig ingested sample favors crania, cervical and lumber vertebrae, and forelimbs; thoracic vertebrae, ribs, and distal limb bones were ingested the least. The BE's skeletal element proportion indices (Table 11) show that:
    - (PC<C) postcranial bones were less frequently ingested than cranial bones
    - (ZE>ST) lower limb bones were ingested slightly more often than upper limb bones
    - (AN>PO) ingested anterior bones greatly outnumber posterior bones
    - (AX<AP) axial bones were less-frequently ingested than appendicular bones

3.1.3. Rabbit deleted-part representation

The coyote deleted more than twice as many bones (MNE 771) as the GHO (MNE 264) and BE (MNE 249), each of which deleted bones in about the same proportion. The relative abundance (Table 10 and Fig. 18) and skeletal element proportion indices (Table 11) demonstrate that:

- The coyote-rabbit deleted bone sample displays a high proportion of deleted ribs, sternebrae, and vertebrae; appendicular and cranial elements show moderate levels of deletion. The coyote's skeletal element proportion indices (Table 11) show that:

- (PC>C) deleted postcranial bones far outnumber cranial bones
- (ZE<ST) lower limb bones were less frequently deleted than upper limb bones
- (AN<PO) anterior bones were deleted slightly less frequently than posterior bones
- (AX>AP) deleted axial bones far outnumber appendicular bones

- The great horned owl-rabbit deleted bone sample shows relatively low levels of deletion; deleted bones include ribs, sternebrae, patellae and thoracic vertebrae. The GHO's skeletal element proportion indices (Table 11) show that:
  - (PC/C) there are too few deleted postcranial and cranial bones to compare
  - (ZE/ST) there are too few deleted lower and upper limb bones to compare
  - (AN<PO) anterior bones were deleted less frequently than posterior bones
  - (AX>AP) deleted axial elements far outnumber appendicular bones
- The bald eagle-rabbit deleted bone sample also shows relatively low levels of bone deletion overall; bones that were occasionally deleted are ribs, sternebrae, cervical and thoracic vertebrae, and patellae. The BE's skeletal element proportion indices (Table 11) show that:
  - (PC/C) there are too few deleted postcranial and cranial bones to compare
  - (ZE=ST) lower and upper limb bones were deleted in equal proportions
  - (AN<PO) anterior bones were deleted less often than posterior bones
  - (AX>AP) axial bones were deleted far more often than appendicular bones

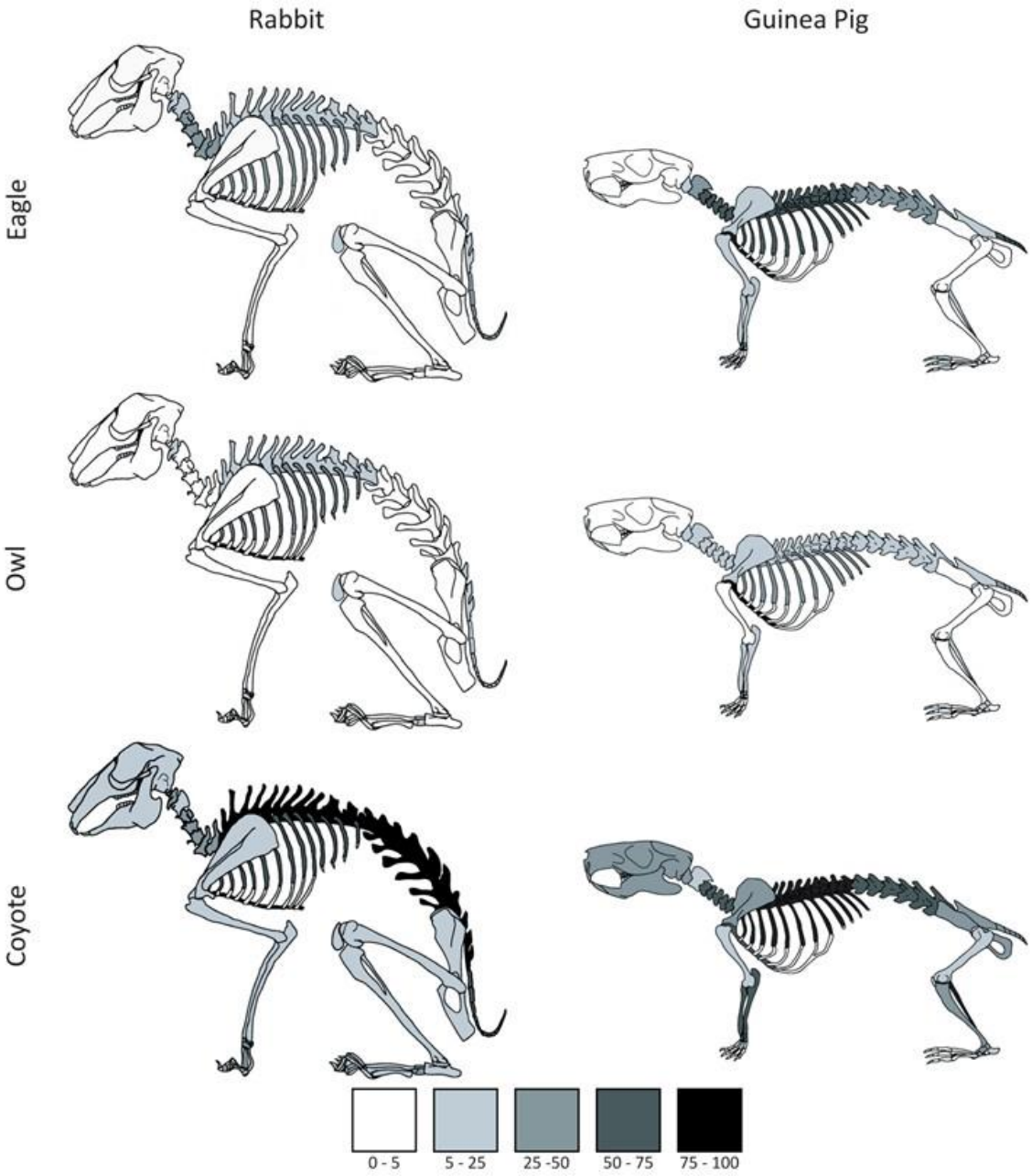


Figure 18: Deleted part frequencies by skeletal element for rabbits and guinea pigs fed to the predators.

3.1.4 Guinea pig deleted-part representation

The coyote deleted the most GP bones (MNE 737), followed by the BE (MNE 543), and GHO (MNE 243). The relative abundance (Table 10 and Fig. 18) and skeletal element proportion indices (Table 11) demonstrate that:

- The coyote-guinea pig deleted sample features deleted cervical and thoracic vertebrae, ribs, sternebrae, radii, and ulnae; cranial bones, scapulae, tibia, and pelves were also regularly deleted, though less frequently than the former group of bones. The coyote's skeletal element proportion indices (Table 11) show that:
  - (PC<C) postcranial bones were deleted less frequently than cranial bones
  - (ZE>ST) lower limb bones were deleted more frequently than upper limb bones
  - (AN=PO) anterior and posterior limb bones were deleted in about equal proportions
  - (AX>AP) deleted axial bones far outnumber deleted appendicular bones
- The great horned owl-guinea pig deleted sample displays relatively low levels of deletion; bones that were deleted somewhat regularly include ribs, sternebrae, cervical, thoracic, and lumbar vertebrae. The GHO's skeletal element proportion indices (Table 11) show that:
  - (PC/C) there are too few deleted postcranial and cranial bones to compare
  - (ZE/ST) there are too few deleted upper and lower limb bones to compare

- (AN>PO) anterior bones were deleted more frequently than posterior bones
- (AX>AP) axial bones were deleted more frequently than appendicular bones

- The bald eagle-guinea pig deleted sample features cervical, thoracic, and lumbar vertebrae as well as ribs, sternebrae, and forelimb bones. The BE's skeletal element proportion indices (Table 11) show that:
  - (PC>C) postcranial bones were deleted more frequently than cranial bones
  - (ZE<ST) lower limb bones were deleted less frequently than upper limb bones
  - (AN>PO) anterior bones were deleted far more frequently than posterior bones
  - (AX>AP) axial bones were deleted far more frequently than appendicular bones

3.2. Bone relative abundance and bone structural density

For each rabbit and GP sample, there is a positive relationship between relative abundance and structural density (Fig. 19). However, only the GHO-rabbit (r_2=0.629, p=<0.01) and coyote-GP (r_2=0.552, p=0.01) samples exhibit positive and significant relationships between bone survivorship and density. All other prey samples indicate positive but weak, non-significant relationships between the two variables.

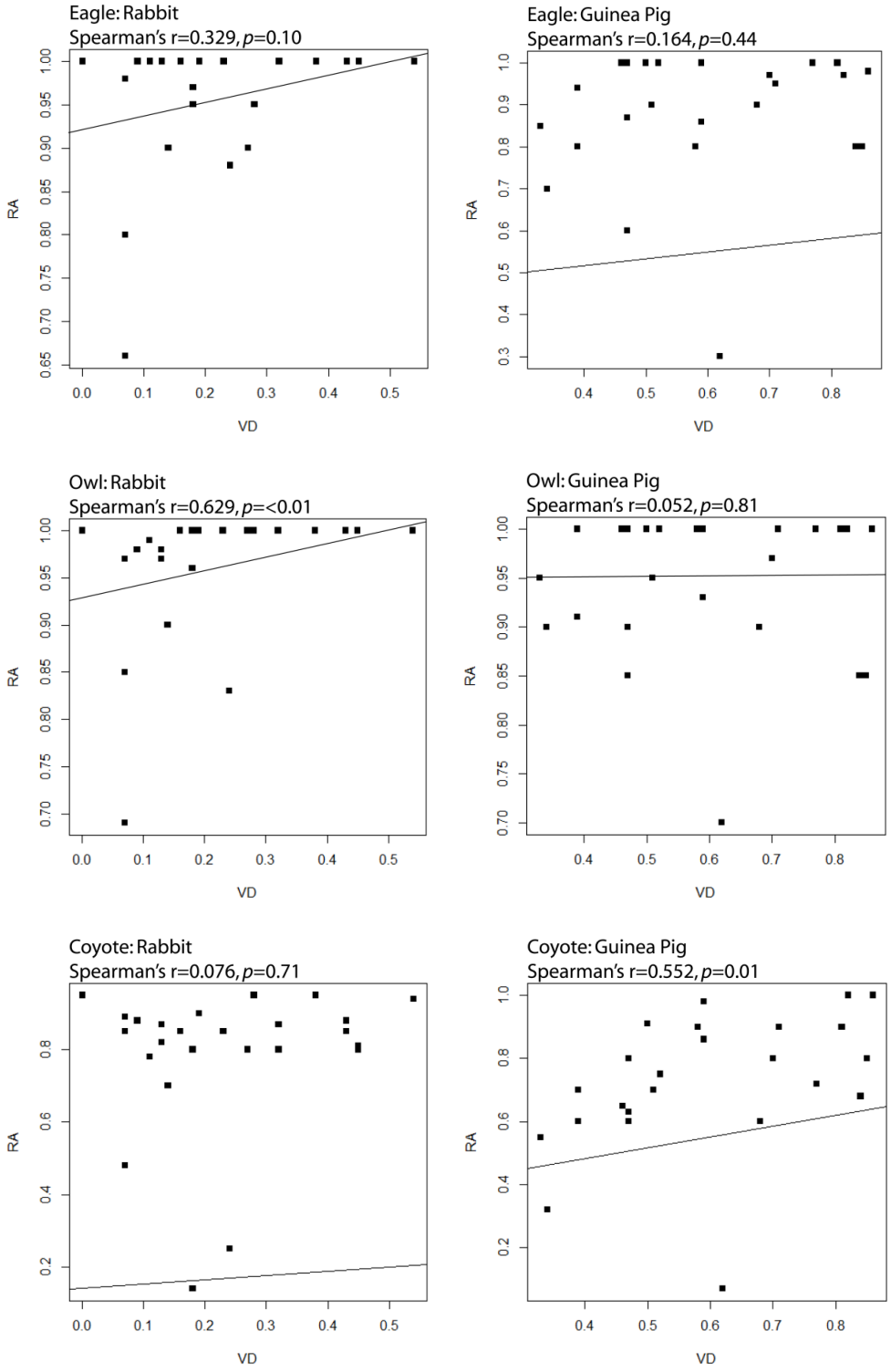


Figure 19: The relationship between bone density (volume density) and skeletal

element frequency (relative abundance) for the rabbit and guinea pig assemblages.

3.3. Bone fragmentation and breakage

Fragmentation indices (NISP/MNE) and whole bone percentage (%whole) were calculated for each of the samples (Table 12). The non-ingested rabbit and GP samples reveal low levels of fragmentation overall, whereas ingested prey remains show a marked increase in the number of fragmented bones (Table 12). In both the non-ingested and ingested samples, small, compact bones – such as podial elements and teeth – are characteristically whole. When these bones are excluded from analyses (Table 12), the rate of fragmentation increases substantially for both ingested and non-ingested specimens, highlighting the fact that cranial, axial, and long bone elements were often fragmented. For each prey sample, specific bone fragment categories and counts for both non-ingested and ingested specimens are shown in Appendix D; element completeness is summarized below:

- Crania: Complete crania are absent from the ingested samples. Among the non-ingested samples, 40% and 20% of the BE-rabbit/GP crania and 20% and 10% of the GHO-rabbit/GP crania are complete by NISP. The coyote did not yield any complete crania.
- Mandibles: Complete mandibles are somewhat rare. All ingested mandibles (except for one coyote-GP mandible) are fragmented. Completeness for total non-ingested mandibles are 50% and 10% of BE-rabbit/GP mandibles, 35%

and 45% of GHO-rabbit/GP mandibles, and 0% and 5% of coyote-rabbit/GP mandibles by NISP.

- Vertebrae: The frequencies of complete vertebrae (cervical, thoracic, and lumbar) vary between the samples. There are no complete vertebrae among the ingested raptor and the coyote-rabbit samples and only one ingested coyote-GP complete vertebrae (6% of NISP). For the non-ingested samples, the BE produced 39% and 43% and the GHO produced 63% and 24% complete rabbit and GP vertebrae by NISP respectively. The coyote did not produce any complete non-ingested vertebrae.
- Ribs: Complete ribs are extremely scarce among all samples. There are no complete ribs among the ingested samples. Among the non-ingested samples the BE yielded 8% and 0%, the GHO yielded 8% and 3% complete rabbit and GP ribs by NISP respectively; 100% (a sample of only 1) and 0% of coyote rabbit and GP ribs by NISP are complete.
- Innominates: Complete innominates are absent from the ingested samples and there are few among the non-ingested bones. For the non-ingested samples, the BE yielded 20% and 12% and the GHO yielded 16% and 11% complete rabbit and GP innominates by NISP respectively; there are no complete innominates among the coyote samples.
- Long bones: With the exception of one ingested coyote-GP humerus, there are no complete long bones (humerus, radius, ulna, femur, tibia, and fibula) in the ingested samples. Between the non-ingested samples, the BE yielded

92% and 81% and the GHO yielded 99% and 83% complete rabbit and GP long bones by NISP respectively; there are no complete long bones among the coyote samples.

- Autopodia: All autopodial (metapodials, phalanges, astragali, and calcanei) bones in the non-ingested samples are complete. Among the ingested samples, the BE yielded 91% and 51%, the GHO yielded 84% and 91%, and the coyote yielded 63% and 84% complete rabbit and GP autopodia by NISP respectively. Further, among the ingested raptor samples, astragali, calcanei, and metacarpals are nearly all complete. The number of coyote ingested complete astragali and calcanei ranges between 66-75% by NISP among the rabbit and GP samples. Complete metacarpals range between 42-81% by NISP for all ingested predator samples; complete ingested metatarsals vary between 25% (coyote-rabbit) to 79% (GHO-GP) by NISP for all ingested predator samples. Frequencies of complete ingested phalanges range from 100% and 18% for the BE, 75% and 94% for the GHO, and 57% and 86% for the coyote-rabbit and GP samples by NISP.

Table 12: Bone fragmentation and specimen size for rabbits and guinea pigs fed to the predators: fragmentation[a] (NISP/MNE all bones), fragmentation[b] (NISP/MNE excluding podia and teeth), %whole[a] (all bones), %whole[b] (long bones only), minimum, maximum, standard deviation, and mean size of specimens, %<10 and %<20 (percent of specimens less than 10 and 20mm).

Rabbit	Fragmen-tation[a]	Fragmen-tation[b]	%Whole[a]	%Whole[b]	Min. length	Max. length	Mean length	SD length	%<10	%<20
Eagle[1]	1.06	1.14	76.8	92.3	2.1	94.9	29.7	26.8	24.6	58.9
Eagle[2]	1.44	1.68	47.1	0	1.5	31.8	7.0	6.0	77.8	97.2
Owl[1]	1.05	1.18	85.6	98.7	2.5	99.7	31.7	28.0	32.8	56.7
Owl[2]	1.92	2.63	24.1	0	1.5	44.5	9.1	8.3	55.6	83.3
Coyote[1]	1.10	2.93	87.3	0	1.9	45.7	15.6	10.3	35.7	67.9
Coyote[2]	1.83	2.65	25.1	0	1.4	37.8	7.9	7.4	66.2	86.3
Guinea Pig										
Eagle[1]	1.06	1.17	78.4	80.7	1.6	62.7	15.8	14.1	48.2	78.1
Eagle[2]	1.30	1.56	24.0	0	1.0	26.1	6.0	4.6	88.4	96.3
Owl[1]	1.05	1.12	78.5	83.1	1.6	60.8	16.1	14.7	51.9	75.9
Owl[2]	1.49	1.91	30.5	1.9	1.0	31.7	6.5	5.8	78.3	95.0
Coyote[1]	1.00	-	100.0	-	1.4	17.8	7.7	4.5	66.7	100.0
Coyote[2]	1.64	2.73	42.1	1.3	1.0	34.8	5.2	5.6	78.3	95.9

[1]Non-ingested
[2]Ingested

The majority of all long bones from the ingested samples are fragmented while most of the non-ingested long bones are whole (Table 12). As for specimen lengths, all non-ingested prey remains are longer in average length than the average length of ingested remains (Table 12). The majority of specimens in all ingested samples have a length value of less than 10 mm while the majority of all non-ingested samples have a length value of less than 20 mm (Table 12).

Long bone breakage patterns are presented in Table 13. The breakage patterns among the rabbit and GP non-ingested and ingested prey remains reveal that bones were broken fresh during disarticulation and consumption. Predictably few bones exhibit dry bone breakage patterns.

Table 13: Occurrence of fresh and dry fracture angles, fracture outlines, and fracture edges for ingested and non-ingested long bones for rabbits and guinea pigs accumulated by the predators.

	Fracture angle (%)			Fracture outline				Fracture edge	
	Oblique (fresh)	Right (dry)	Oblique /right	V-shaped (fresh)	Transverse (dry)	Inter-mediate	Transverse /curved	Smooth (fresh)	Jagged (dry)
Eagle									
Rabbit[1]	21 (88)	1 (4)	2 (8)	8 (33)	3 (13)	2 (8)	11 (46)	22 (92)	2 (8)
Rabbit[2]	17 (77)	0 (0)	5 (23)	10 (45)	0 (0)	2 (9)	10 (45)	22 (100)	0 (0)
GP[1]	33 (80)	6 (15)	2 (5)	27 (66)	5 (12)	3 (7)	6 (15)	35 (85)	6 (15)
GP[2]	48 (75)	11 (17)	5 (8)	46 (72)	3 (5)	4 (6)	11 (17)	44 (96)	2 (4)
Owl									
Rabbit[1]	12 (75)	3 (19)	1 (6)	10 (63)	2 (13)	3 (19)	1 (6)	15 (94)	1 (6)
Rabbit[2]	51 (82)	3 (5)	8 (13)	58 (94)	1 (2)	2 (3)	1 (2)	57 (92)	5 (8)
GP[1]	24 (86)	1 (4)	3 (11)	19 (68)	4 (14)	4 (14)	1 (4)	25 (89)	3 (11)
GP[2]	114 (94)	3 (2)	4 (3)	45 (37)	17 (14)	20 (17)	39 (32)	121 (100)	0 (0)
Coyote									
Rabbit[1]	27 (93)	1 (3)	1 (3)	25 (86)	0 (0)	2 (7)	2 (7)	27 (93)	2 (7)
Rabbit[2]	364 (94)	4 (1)	21 (5)	234 (60)	53 (14)	27 (7)	75 (19)	382 (98)	7 (2)
GP[1]	-	-	-	-	-	-	-	-	-
GP[2]	225 (89)	18 (7)	11 (4)	178 (70)	14 (6)	24 (9)	38 (15)	237 (93)	17 (7)

[1]Non-ingested
[2]Ingested

3.4. Bone surface modifications

Bones exhibiting surface modifications are frequent in all samples (Appendix E, F, G); these modifications include punctures, pits, crenulated and

fractured edges, notches, scores, and digested bone. Concerning the rabbit samples, the combined non-ingested and ingested totals of all surface modified bone (including digestion damage) for the BE, GHO, and coyote are 33.4%, 68.5%, and 96.8% of n for each sample. When ingested bones are excluded the frequency of BSMs drops to 21.0%, 2.6%, and 5.4% of n respectively. The combined non-ingested and ingested frequencies of surface modified bones (including digestion damage) for the GP samples are 55.7%, 78.8%, and 98.7% of n for BE, GHO, and coyote samples. When ingested bones are excluded the frequency drops to 13.1%, 8.0%, and 1.4% of n respectively.

Table 14 displays the counts and frequencies of the degrees of digestion for each prey sample. For each of the rabbit and GP samples, the GHO inflicted less digestion damage in comparison to the other predators. A combined 75% of the rabbit and 66%

Table 14: Totals and frequencies of degree of damage caused by digestion for rabbits and guinea pigs accumulated by the predators.

Rabbit	Null (%)	Light	Moderate	Heavy	Extreme
Eagle	11 (4)	51 (18)	89 (32)	94 (34)	33 (12)
Owl	512 (27)	787 (42)	408 (22)	144 (8)	12 (1)
Coyote	194 (6)	535 (15)	1064 (30)	1197 (34)	501 (14)
Guinea pig					
Eagle	34 (5)	138 (20)	251 (36)	207 (30)	71 (10)
Owl	486 (27)	738 (41)	414 (23)	146 (8)	34 (2)
Coyote	112 (5)	352 (17)	644 (31)	697 (33)	276 (13)

of the GP specimens retrieved from the GHO pellets where scored as either "light" or "null" damage. The BE and coyote inflicted similar degrees of damage to the rabbit and GP bones, a combined 66% and 66% for the BE and 64% and 70% for the coyote rabbit and GP remains.

3.4.1. Rabbit bone surface modifications

Rabbits: Digestion damage is the most frequent BSM for each of the rabbit predator samples. For the BE sample very few BSMs (excluding digestion damage) were observed in the ingested portion of the sample (17 modified specimens total, 3.5% of n), the vast majority of surface modified bones were recorded on non-ingested bone (475 modified specimens total, 21.0% of n). The GHO exhibited a different pattern where surface modified bone (excluding digestion) is more evenly distributed between the non-ingested (135 modified specimens total, 4.2% of n) and ingested (146 modified specimens total, 4.6% of n) portions of the sample. For instance, there were 13 and 14 punctured specimens recovered from the GHO non-ingested and ingested samples respectively. For the coyote sample the frequency of surface modified bone is extremely skewed towards the ingested portion (146 modified ingested specimens, 5.1% of n versus 11 modified non-ingested specimens, 0.3% of n), it is important to know however, that over 90% of the coyote sample was recovered from scat and exhibits digestion damage.

BSM frequencies and their anatomical location for each predator sample can be found in Appendix E, F, G:

- Punctures: BE rabbit prey remains exhibit six (0.3% of n) punctures, the GHO 27 (0.8% of n), and the coyote 22 (0.6% of n). There were three specimens with multiple punctures: a coyote-accumulated proximal tibia and GHO generated innominate and crania. The anatomical distribution of punctures is similar between the predator samples; cranial bones, lumber vertebrae, and innominates are commonly punctured elements. All punctures are located on specimens with thin cortical bone and underlying trabecular structures (such as parietals, vertebrae, long bone epiphyses, and ilia). Punctures are absent from compact skeletal elements and portions of bones with thick cortical structures.
    - Table 15 describes the puncture shape, frequency, and size for each prey sample. Oval-shaped punctures were the most common shape in all but one of the prey samples. Triangular and circular punctures were also common but far less frequent than oval punctures. Irregular punctures were typically the largest puncture type by area (mm^2).
- Pits: BE and coyote prey remains exhibit few pits, seven (0.3% of n) and nine respectively (0.2% of n), whereas GHO prey exhibit 47 (1.5% of n) pits. Pits occur on a variety of specimens across the predator samples. Unlike punctures, pits are located on portions of bone with both thin and thick cortical

surfaces and their anatomical distribution is irregular. Approximately 20% of GHO pitted specimens contain multiple pits.

- Crenulated edges: There are 261 (11.5% of n) crenulated bones in the BE prey sample followed by 103 (3.2% of n) GHO and 21 (0.55 of n) coyote crenulated specimens. Though the numbers of crenulated specimens differ widely between samples, the anatomical distribution is similar. The most common crenulated specimens are bones with processes such as the spinous and lateral processes of vertebrae, the mandibular ramus, and portions of the innominate. Ribs also frequently exhibit crenulation.
- Fractured edges: Fractured bone is most frequent in the BE prey sample with 184 (8.1% of n) specimens followed by the 149 coyote (3.8% of n) and 99 GHO (3.1% of n) specimens. The anatomical distribution of fractured bone varies between the samples; all predator samples share fractured crania, mandibles, vertebrae, ribs, and humeri, but the GE and GHO samples contain few fractured hind and distal limb elements. Fractured limb bones are far more common in the coyote sample. There is also a substantial difference in the number of fractured bones retrieved from the ingested portion of the samples, where far fewer fractured bones were retrieved from the BE sample (eight, 2.9% of n) in comparison to the GHO (67, 3.5% of n) and coyote (140, 3.9% of n) samples.

- Notches: Two notches were recorded among all predator samples, both were found in the BE prey remains. The notches are located on the mid-shaft portions of a humerus and tibia.
- Scores: Relatively few scores were recorded among the prey samples. Scored bone is most frequent in the BE sample (15, 0.7% of n) followed by the coyote (eight, 0.2% of n) and GHO (five, 0.2% of n,) samples. There is one BE bone which contains multiple scores; all other scores were unaccompanied.
- Digestion: See section “Rabbit ingested-part representation” for description and distribution of digested bone.

Table 15: Puncture type, frequency, size, and standard deviation occurring on rabbit and guinea pig bones accumulated by the predators.

Eagle

Rabbit						Guinea Pig				
Puncture Type	(%) Punctures	Min. mm^2	Max. mm^2	Mean mm^2	Stand. Dev.	(%) Punctures	Min. mm^2	Max. mm^2	Mean mm^2	Stand. Dev.
Circular	-	-	-	-	-	2 (15.4)	3.2	5.9	4.6	0.6
Irregular	1 (16.6)	3.2	3.2	3.2	0.0	4 (30.8)	2.2	4.9	3.6	1.2
Oval	4 (66.7)	1.5	5.1	2.9	1.9	6 (46.2)	1.7	6.0	3.3	1.2
Rectangular	-	-	-	-	-	-	-	-	-	-
Triangular	1 (16.6)	1.4	1.4	1.4	0.0	1 (7.7)	3.0	3.0	3.0	0.0
Total (Avg)	6	2.0	3.2	2.5	-	13	2.5	5.0	3.6	-

Owl

Rabbit						Guinea Pig				
Puncture Type	(%) Punctures	Min. mm^2	Max. mm^2	Mean mm^2	Stand. Dev.	(%) Punctures	Min. mm^2	Max. mm^2	Mean mm^2	Stand. Dev.
Circular	4 (14.8)	2.3	4.7	3.5	1.9	2 (20.0)	1.7	1.9	1.8	1.2
Irregular	4 (14.8)	2.2	4.5	3.6	1.8	-	-	-	-	-
Oval	12 (44.4)	1.1	7.0	3.3	1.7	4 (40.0)	1.8	3.8	2.8	1.4
Rectangular	2 (7.4)	1.3	2.3	1.8	1.7	-	-	-	-	-
Triangular	5 (18.5)	1.7	4.8	3.1	1.8	4 (40.0)	2.2	4.9	3.5	1.3
Total (Avg)	27	1.7	4.7	3.1	-	10	1.9	3.5	2.7	-

Coyote

Rabbit						Guinea Pig				
Puncture Type	(%) Punctures	Min. mm^2	Max. mm^2	Mean mm^2	Stand. Dev.	(%) Punctures	Min. mm^2	Max. mm^2	Mean mm^2	Stand. Dev.
Circular	6 (27.2)	2.5	5.8	3.8	1.3	1 (50.0)	3.5	3.5	3.5	0.0
Irregular	1 (4.5)	7.3	7.3	7.3	0.0	-	-	-	-	-
Oval	14 (63.6)	1.6	8.8	4.3	1.8	1 (50.0)	4.4	4.4	4.4	0.0
Rectangular	1 (4.5)	4.4	4.4	4.4	0.0	-	-	-	-	-
Triangular	-	-	-	-	-	-	-	-	-	-
Total (Avg)	22	4.0	6.6	5.0	-	2	4.0	4.0	4.0	-

3.4.2. Guinea pig bone surface modifications

As in the rabbit samples, digestion damage is the most common BSM for each of the GP samples. For the BE sample only 11 (0.6% of n) BSMs (excluding digestion damage) were observed in the ingested portion of the sample, the vast majority of surface modified bones were recorded on non-ingested bone totaling 222 (13.0% of n). The distribution of BSMs in the GHO sample is also skewed toward the non-ingested portion with 162 (6.0% of n) and only 64 (2.4% of n) found in the ingested portion. BSMs in the coyote sample (excluding digested damage) are most common in the ingested portion of the sample with 38 (1.4% of n); there are no bone modifications in the non-ingested portion of the sample.

BSM frequencies and their anatomical locations for each predator sample can be found in Appendix E, F, G:

- Punctures: BE prey remains feature 13 (0.8% of n) punctures followed by 10 (0.4% of n) for the GHO and two (0.2% of n) for the coyote. Of note is the substantial decrease in the number of GHO and coyote punctures but the slight increase in the BE sample in comparison to the rabbit puncture frequencies. There were no specimens with multiple punctures. The anatomical distribution of punctures is similar between the GP and rabbit samples as punctures are located on specimens with thin cortical bone and underlying trabecular structures but absent from bone with thick cortical surfaces.

- Table 15 describes the puncture shape, frequency, and size for each predator and prey sample. Oval shaped punctures are the most common among the prey samples. Irregular punctures are the second most common shape among the BE prey while triangular punctures are tied in frequency with oval among GHO prey. Rectangular punctures were not observed among any of the samples. The largest shaped puncture was different for each sample.

- Pits: GHO prey remains exhibit only eight (0.3% of n) pits, far less than the pits accumulated in the rabbit remains. There are five pitted specimens in both the BE and coyote samples (0.3% and 0.2% of n respectively). Approximately 12% of all pitted specimens contain multiple pits. As was observed in the rabbit prey samples, pits are located on portions of bone with both thin and thick cortical surfaces and their anatomical distribution is irregular.
- Crenulated edges: The GHO exhibits 124 (4.6% of n) specimens with crenulated edges while the BE features 115 (6.8% of n) and the coyote has eight (0.3% of n). The imbalance between the raptors and coyote crenulated remains is evident in both the rabbit and GP samples, however, the anatomical distribution of crenulation is similar. Like the rabbit samples, the most common crenulated specimens are bones with processes and ribs.
- Fractured edges: There are 95 (5.6% of n) fractured specimens in the BE sample, followed by 80 (3.0% of n) in the GHO and 22 (0.8% of n) in the

coyote samples. There are fewer BE and coyote fractured specimens in the GP sample in contrast to the rabbit samples. The anatomical distribution of fractures differs between the raptor and coyote samples as the coyote exhibits mostly cranial and long bone fractures and the raptors feature an irregular distribution of fractures across multiple elements. There is also a sizable difference in the number of fractured bones retrieved from the ingested portions of the samples, where far fewer fractured bones were retrieved from the BE sample (4, 0.6% of n) in comparison to the GHO (31, 1.6% of n) and coyote (22, 0.8% of n) samples.

- Notches: Two notches were recorded among all predator samples, both were found in the GHO prey remains. The notches are located on the mid-shaft portion of a femur and a long bone shaft fragment.
- Scores: There are few scored specimens in the predator assemblages, five (0.3% of n) BE, three (0.1% of n) GHO, and one (0.0% of n) coyote score. Two BE specimens contain multiple scores. There are multiple scored innominates in both the BE and GHO samples.
- Digestion: See section “Guinea pig ingested -part representation” for description and distribution of digested bone.

4. DISCUSSION

4.1. Non-ingested-, ingested-, and deleted-part profiles

Table 16 shows Chi-square test of independence values for head-to-head comparisons between each prey samples' non-ingested-, ingested-, deleted-, and fragmented-part profiles. The comparisons are discussed below:

Non-ingested-part profiles: With one exception (the BE-rabbit and GHO-GP profiles), the intra- and interspecific comparisons are significantly different at the 0.05 level (Table 16a). In the case of the exception, the BE ingested far fewer rabbit bones in comparison to the number of GP bones swallowed by the GHO, but each deleted a similar number of matching skeletal elements. This dynamic is likely why these two disparate predator and prey profiles appear similar. With one exception, both the intra- and interspecific anatomical profiles are distinct by accumulating agent.

The intraspecific non-ingested-part profiles demonstrate that the predators produced different prey anatomical distributions based on prey type. The interspecific profiles are also primarily different when comparing between the predator samples. These differences reveal that the predators generate non-ingested-part profiles that are (1) distinctive from each other and (2) differ intraspecifically based on prey type.

Ingested-parts profile: The intra- and interspecific ingested-parts profiles are statistically different at the 0.05 level for all comparisons (Table 16b). The predators ingested distinct patterns of bone by both prey and predator type.

The GHO and coyote each ingested many more bones than the BE, but the profiles of ingested bones are not similar in any way. There is a clear difference in the number and anatomical profile of bone ingested by the BE. The intra- and interspecific differences of ingested prey bones completely differ between predators.

Deleted-parts profile: All but one of the sample comparisons is significantly different at the 0.05 level (Table 16c). The GHO-rabbit/GP test statistic reveals that the comparison of deleted bones is not significantly different while all other intra- and interspecific comparisons are unique. Only the GHO deletes similar types and proportions of rabbit and GP bones.

The BE and coyote deleted different patterns of bones depending on the type of prey. This is at least partially due to the variable numbers of bones based on prey type that were subjected to mastication and digestion by the BE and coyote, whereas the GHO swallowed and deleted similar patterns of prey bones. All interspecific comparisons of deleted bones reveal differences signifying that the BE, GHO, and coyote selectively removed distinct portions of their preys' remains.

With a few exceptions, the non-ingested, ingested, and deleted-part profiles of the prey samples are distinctive. The coyote frequently consumed the entire rabbit or GP carcass, occasionally leaving the cranium and hind limbs of its prey. The near-total consumption of prey by the coyote resulted in a substantial

number of ingested and deleted bones but few non-ingested bones. The GHO also ingested a large portion of both rabbit and GP bones, especially axial and forelimb elements, but deleted far fewer bones than the coyote. The elevated frequency of bone deletion by the coyote likely reflects the effects of mastication and subsequent digestion as many more coyote ingested-bones were reduced to small, unidentifiable fragments. Conversely, ingested rabbit and GP bones retrieved from GHO pellets were often fragmented whereas non-ingested remains were typically left whole. The BE ingested fewer rabbit and GP bones than the GHO and deleted bones more frequently, especially axial elements. The BE also fractured fewer ingested bones and more often fractured non-ingested bones. The differences in the frequencies of deleted bones between the BE and GHO is likely the result of the more robust digestive crop of the BE as well as the tendency to fracture prey skeletal elements while feeding (see Tables 5 and 9 for degree of digestion and predator comparisons). Due to these feeding and digestive differences between the predators, the parts profiles of the prey samples are distinctive.

4.2. Bone relative abundance and volume density

As expected, the positive correlations between bone relative abundance and volume density for each of the prey samples indicate that less robust skeletal elements were more often deleted (through fragmentation and digestion) than

robust bones. Vertebrae, ribs, and long-bone epiphyses are the bone and bone portions that were most often deleted across all samples.

The GHO-rabbit and coyote-GP samples demonstrate statistically significant relationships between bone abundance and density. However, the two assemblages are not particularly similar in terms of individual bone survivorship (Fig. 16). The GHO-rabbit sample is characterized by the excellent preservation of robust bones with moderate deletion of the less robust bones whereas the coyote-GP sample exhibits deletion across all elements with less robust bones exhibiting an extreme degree of loss. The GHO-rabbit and coyote-GP samples represent the extremes in the positive correlation between relative abundance and volume density: good preservation of robust elements or poor preservation of less-robust bones. The other prey assemblages fall somewhere between these two extremes. These results indicate that bone density is a factor in bone survivorship for both prey taxa regardless of predator.

4.3. Bone fragmentation and breakage

Table 16d shows Chi-square test of independence values for head-to-head comparisons between each prey samples' non-ingested fragmentation profile. All sample comparisons, except for the coyote-rabbit/GP fragmentation comparison, are significantly different at the 0.05 level. Except for the coyote samples, the assemblages are not similar in terms of the anatomical patterning of fragmentation. Only the coyote fragmented the rabbits and GP in similar ways.

Both raptors fractured more rabbit than GP bones. However, the anatomical pattern of fractured bones differs between the raptor samples as well as between the intraspecific raptor prey comparisons. Non-ingested bones were often left whole by the GHO and bones that were ingested were frequently fractured, albeit less so with GP bones. Conversely, the BE often fractured non-ingested bones and deleted the bones that were ingested, deleting many more GP bones but fracturing more rabbit bones on the whole. These fragmentation differences are further evidence to suggest that BE and GHO consume prey carcasses differently based on type.

The long bone breakage patterns of non-ingested bone exhibited by each assemblage closely match the 'green' breakage pattern of the small mammals accumulated by Verreaux's eagles reported by Armstrong and Avery (2014) and the fresh breakage sample of Fontbrégoua studied by Villa and Mahieu (1991). There were no breakage differences in terms of prey species. Like their application to large mammal accumulations, these results support the notion that long bone breakage profiles can be used to deduce the origin of breakage in small mammal assemblages.

Table 16: (A) Non-ingested-, (B) ingested-, (C) deleted-, and (D) fragmented-part (non-ingested samples) profiles for rabbits and guinea pigs accumulated by the predators; bold values are *not* significant at the 0.05 level.

16a	**Non-ingested-part profile**						**16b**	**Ingested-part profile**				
	BE-GP	GHO-rabbit	GHO-GP	Coyote-rabbit	Coyote-GP			BE-GP	GHO-rabbit	GHO-GP	Coyote-rabbit	Coyote-GP
BE-rabbit	χ^2=134.5 *p* =<0.01	χ^2=116.4 *p* =<0.01	**χ^2=33.8 *p* =0.33**	χ^2=252.0 *p* =<0.01	χ^2=136.6 *p* =<0.01		BE-rabbit	χ^2=90.1 *p* =<0.01	χ^2=81.2 *p* =<0.01	χ^2=86.6 *p* =<0.01	χ^2=112.6 *p* =<0.01	χ^2=127.8 *p* =<0.01
BE-GP	-	χ^2=77.4 *p* =<0.01	χ^2=101.5 *p* =<0.01	χ^2=116.4 *p* =<0.01	χ^2=139.2 *p* =<0.01		BE-GP	-	χ^2=81.3 *p* =<0.01	χ^2=183.3 *p* =<0.01	χ^2=94.9 *p* =<0.01	χ^2=141.9 *p* =<0.01
GHO-rabbit	-	-	χ2=58.8 *p* =<0.01	χ2=117.9 *p* =<0.01	χ2=172.3 *p* =<0.01		GHO-rabbit	-	-	χ^2=45.2 *p* =0.05	χ^2=147.7 *p* =<0.01	χ^2=236.1 *p* =<0.01
GHO-GP	-	-	-	χ2=204.3 *p* =<0.01	χ2=147.3 *p* =<0.01		GHO-GP	-	-	-	χ^2=100.2 *p* =<0.01	χ^2=119.6 *p* =<0.01
Coyote-rabbit	-	-	-	-	χ2=55.8 *p* =<0.01		Coyote-rabbit	-	-	-	-	χ^2=41.1 *p* =0.05

16c	**Deleted-part profile**						**16d**	**Fragmented-part profile (non-ingested bones)**				
	BE-GP	GHO-rabbit	GHO-GP	Coyote-rabbit	Coyote-GP			BE-GP	GHO-rabbit	GHO-GP	Coyote-rabbit	Coyote-GP
BE-rabbit	χ^2=93.4 *p* =<0.01	χ^2=52.1 *p* =<0.01	χ^2=71.4 *p* =<0.01	χ^2=134.1 *p* =<0.01	χ^2=189.0 *p* =<0.01		BE-rabbit	χ^2=131.3 *p* =<0.01	χ^2=180.4 *p* =<0.05	χ^2=236.4 *p* =<0.01	χ^2=422.8 *p* =<0.01	χ^2=471.5 *p* =<0.01
BE-GP	-	χ^2=56.2 *p* =<0.01	χ^2=40.9 *p* =0.05	χ^2=123.2 *p* =<0.01	χ^2=108.8 *p* =<0.01		BE-GP	-	χ^2=68.3 *p* =<0.01	χ^2=97.7 *p* =<0.01	χ^2=353.9 *p* =<0.01	χ^2=415.4 *p* =<0.01
GHO-rabbit	-	-	**χ^2=25.4 *p* =0.61**	χ^2=76.3 *p* =<0.01	χ^2=142.1 *p* =<0.01		GHO-rabbit	-	-	χ^2=93.9 *p* =<0.01	χ^2=346.7 *p* =<0.01	χ^2=408.2 *p* =<0.01
GHO-GP	-	-	-	χ^2=97.1 *p* =<0.01	χ^2=115.2 *p* =<0.01		GHO-GP	-	-	-	χ^2=234.8 *p* =<0.01	χ^2=295.1 *p* =<0.01
Coyote-rabbit	-	-	-	-	χ^2=176.1 *p* =<0.01		Coyote-rabbit	-	-	-	-	**χ^2=24.3 *p* =0.50**

4.4. Bone surface modifications

Generally, each predator exhibits different frequencies and locations of BSMs (Appendix E, F, G). However, not all BSM frequencies and locations differ between the samples; there are some similarities in terms of type and frequency of modification. Table 17 shows the *p*-value results of binomial logistic regression analyses of intra- and interspecific predator and prey comparisons for each BSM and Fig. 20 graphically depicts the probability of observing each BSM

as well as the degree of similarity or difference among the individual predator and prey samples.

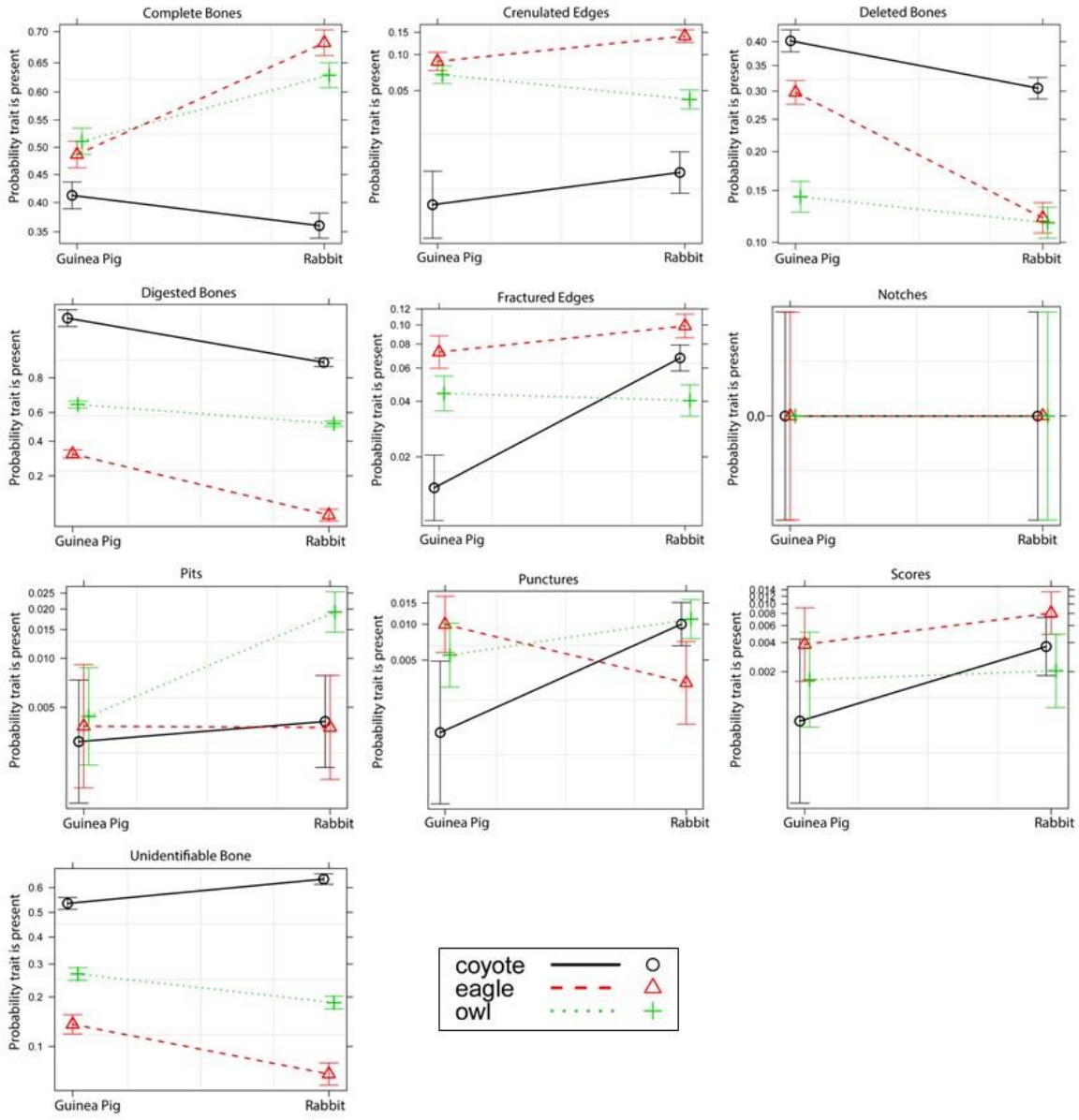


Figure 20: Comparisons of bone surface modification and sample attribute frequencies for each predator and prey group; whiskers represent 95% confidence intervals; lines close to parallel signify correspondence in

the probability that the trait is present between the prey samples for a particular predator, angled lines signify the opposite.

4.4.1. Intraspecific predator comparisons

Intraspecific predator comparisons (Table 17 and Fig. 20) reveal that the frequency of observing notches and scores are not significantly different between any of the predator relationships, all *p*-values are >0.05. For pits and digestion, only one predator comparison displays significant frequency differences for each modification: for pits the GHO-rabbit/GP and for digestion the BE-rabbit/GP comparisons. There are two significant frequency differences each for punctures, crenulated, and fractured edge surface modifications: for punctures and fractured edges the coyote- and BE-rabbit/GP, and for crenulated edges the BE- and GHO-rabbit/GP.

Table 17: Intra- and interspecific predator comparisons for each bone surface modification; bold values are significant at the 0.05 level.

Intraspecific predator comparisons								
Prey	Predator	Puncture	Pits	Crenulate	Fractured	Notch	Scores	Digested
GP/rabbit	coyote	**0.00**	0.61	0.11	**0.00**	1.00	0.09	0.08
GP/rabbit	eagle	**0.02**	0.98	**0.00**	**0.01**	1.00	0.15	**0.00**
GP/rabbit	owl	0.06	**0.00**	**0.00**	0.56	1.00	0.77	0.07
Interspecific predator comparisons								
GP	coyote/egale	**0.02**	0.94	**0.00**	**0.00**	1.00	0.22	**0.00**
GP	coyote/owl	0.13	0.80	**0.00**	**0.00**	1.00	0.67	**0.00**
GP	eagle/owl	0.33	0.97	0.10	**0.00**	1.00	0.48	**0.00**
rabbit	coyote/egale	**0.04**	0.98	**0.00**	**0.00**	1.00	0.16	**0.00**
rabbit	coyote/owl	0.94	**0.00**	**0.00**	**0.00**	1.00	0.57	**0.00**
rabbit	eagle/owl	**0.02**	**0.00**	**0.00**	**0.00**	1.00	**0.02**	**0.00**

In sum, 13 of the 21 intraspecific BSM (Table 17) comparisons are not significantly different, specifically the notch and score comparisons, and to lesser extent, pits and digestion. However, eight BSM frequency comparisons differ significantly between the rabbit and GP samples even though they were modified by a single predator. This signifies that prey size is an important taphonomic variable when assessing small mammal accumulations, particularly in relation to punctures, pits, digestion, crenulated, and fractured edge modification frequencies. But there is not a single intraspecific BSM comparison where all predators exhibit statistically significant modification frequency differences by prey type. For instance, puncture frequency is significantly different for both BE- and coyote-rabbit/GP relationships, but not for GHO. Conversely, pit frequency differs significantly for GHO-rabbit/GP but not for BE and coyote prey. Ultimately, these results offer further confirmation that the predators in this study consume their prey differently, however, it is the totality of BSM frequencies – coupled with other taphonomic attributes – that illuminates this fact as opposed to the assessment of any single BSM.

4.4.2. Interspecific predator comparisons

Like the intraspecific predator comparisons, interspecific predator comparisons (Table 17 and Fig. 20) reveal a mixture of BSM similarities and differences between the prey samples.

Among all GP samples nine of 21 BSM comparisons (Table 17) are significantly different. There are no significant differences between the number of pits, scores, or notches the coyote, GHO, or BE made on GPs, except when the coyote is compared with the BE. However, all digested, crenulated, and fractured edge comparisons are significantly different at the 0.05 level, the only exception is the BE/GHO crenulated edge frequency comparison. There are more significantly different BSM comparisons among the rabbits than among the GP samples, 13 of 21 comparisons. Between the rabbit samples, there are no significant differences between notch frequencies, and only the BE/GHO comparison is significantly different for scores. For punctures, pits, digested, crenulated, and fractured edges the frequencies of bone damage are significantly different between predator samples. Only the coyote/GHO puncture and coyote/BE pit comparisons are minor.

The surface modification frequency variations between the raptor rabbit and GP samples may be due to prey size differences. A possible explanation is that in order to reduce the larger rabbits down to edible portions, the raptors routinely manipulate the carcasses with their beaks and talons in order to disarticulate portions, resulting in increased BSMs. The GPs, being only about one third the size of rabbits, could more easily be reduced to comestible portions without inflicting bone damage. Nevertheless, there are patterns of BSM differences among both prey groups further signifying that these small mammal accumulators do not handle their prey in a uniform way.

4.4.3. Bone surface modification profiles

To determine if the differences between the BSM profiles of each sample are sufficient to distinguish between prey and predator accumulations, a series of principal component analyses (PCA) were conducted utilizing the BSM categories (punctures, pits, scores, notches, digested, crenulated, and fractured edges) and other sample attributes (deleted, complete, and unidentifiable bone frequencies) of each prey sample. Figure 21 is a PCA plot using only the BSM categories and Table 18 shows component loadings. Only the coyote-GP and BE-rabbit samples represent discernable clusters. The GHO- and BE-GP clusters overlap as do the GHO-and coyote-rabbit clusters, consequently these groups are largely indistinguishable from each other. Though the overlapping samples do not separate by predator, they do differentiate by prey (i.e. rabbit or GP).

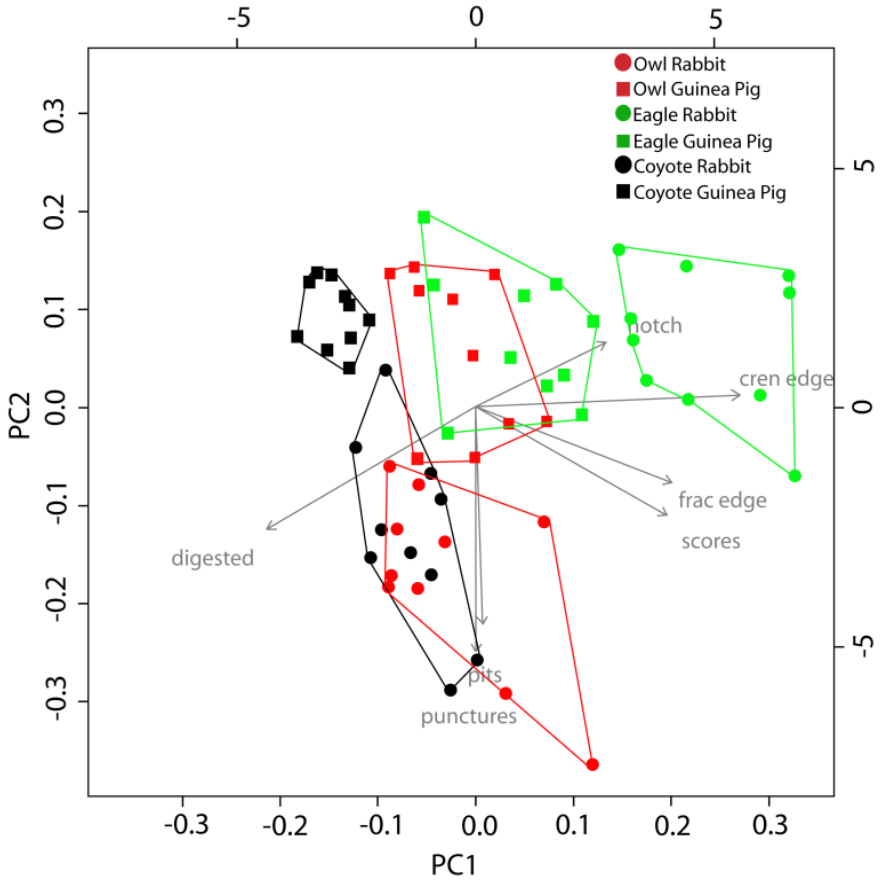


Figure 21: Principal components plot of the bone surface modification values for each predator sample.

Figure 21 is a PCA plot that incorporates all seven BSM categories as well as the additional sample attributes; Table 18 shows the component loadings for this plot. The matrix generated by these PCA loadings results in greater separation of predator and prey groups with minimal overlap between clusters. Only the GHO-rabbit/GP clusters share space, all other predator and prey clusters are separate and distinctive. The predator and prey separation

demonstrated in Fig. 7 suggests that: 1) the BSM profiles of the GHO-rabbit/GP samples are to some extent similar (though there is sizable

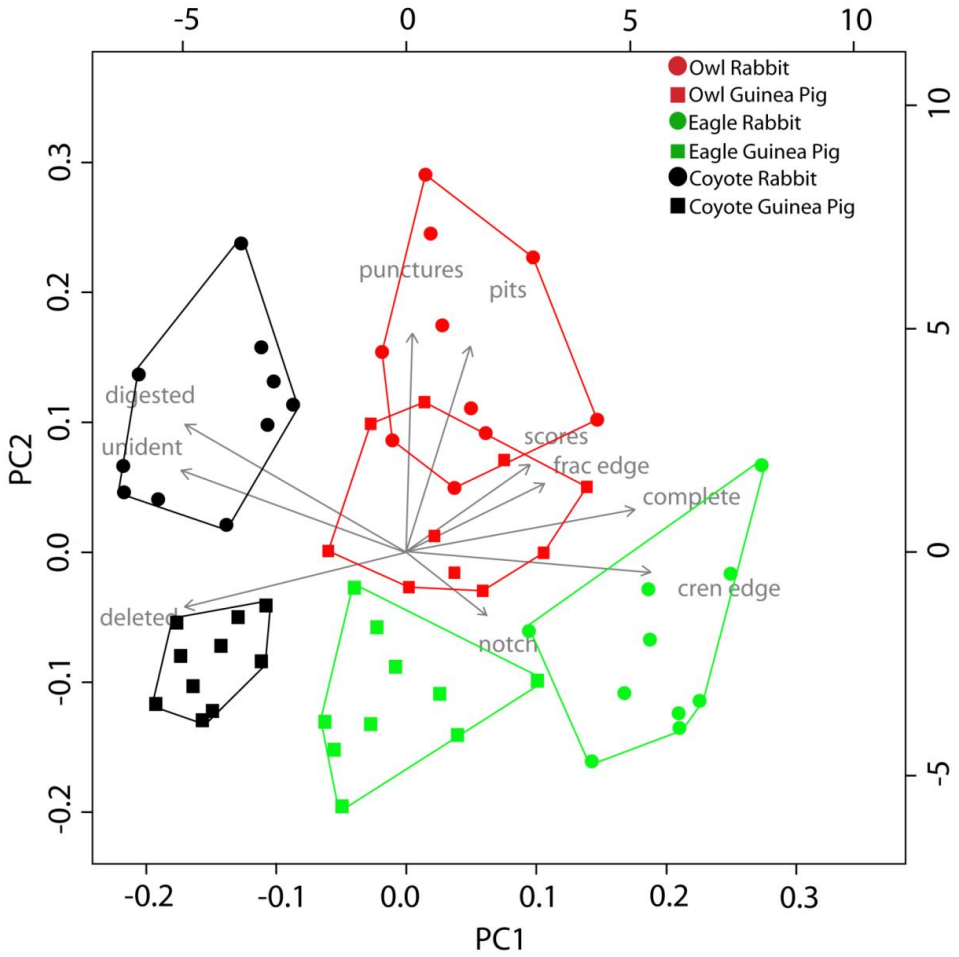


Figure 22: Principal components plot of the bone surface modification values and additional sample attributes for each predator sample.

separation between them) and therefore not as distinctive as the other predator samples, but that 2) the observed taphonomic attributes (BSMs and sample attributes) are sufficient to differentiate between small mammals of different sizes accumulated by differing predators.

Table 18: Principal component values for (1) bone surface modifications only (Fig. 21) and (2) bone surface modification and addition attributes (Fig. 22) for the predator samples.

Importance of components:	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
(1) Standard deviation	1.53788	1.27956	0.96579	0.84881	0.77724	0.71680	0.47593	-	-	-
(1) Proportion of Variance	0.99787	0.23390	0.13325	0.10293	0.08630	0.07340	0.03236	-	-	-
(1) Cumulative Proportion	0.33787	0.57176	0.70502	0.80794	0.89424	0.96764	1.00000	-	-	-
(2) Standard deviation	1.99774	1.32719	1.12709	0.92492	0.80350	0.75686	0.62618	0.51777	0.41127	0.27205
(2) Proportion of Variance	0.39910	0.17614	0.12702	0.08555	0.06456	0.05728	0.03921	0.02681	0.01691	0.00740
(2) Cumulative Proportion	0.39910	0.57524	0.70227	0.78782	0.85238	0.90967	0.94888	0.97568	0.99260	1.00000

4.4.4 Extent of digestion

Table 19 shows the *p*-value results of binomial logistic regression analyses of intra- and interspecific comparisons of the frequency of degrees of digestion. All but one of the intraspecific comparisons (extreme degree, GHO) is not significant, indicating that the degree of digestion inflicted by each predator does not vary by prey size. The predators inflict the same amount of digestion damage on rabbits as they do GPs. However, interspecific comparisons reveal that the degree of digestion damage caused by the GHO is significantly less than the BE and coyote, and that the degree of digestion between the BE and coyote is not significantly different. These results are in accordance with Andrews (1990) who noted that owl digestion is typically less extensive than other diurnal raptors and carnivores.

Table 19: Intra- and interspecific predator comparisons for the degree of damage caused by digestion for rabbits and guinea pigs accumulated by the predators; bold values are significant at the 0.05 level.

Intraspecific predator comparisons						
Prey	Predator	None	Light	Moderate	Heavy	Extreme
GP/rabbit	coyote	0.78	0.12	0.71	0.54	0.26
GP/rabbit	eagle	0.55	0.63	0.26	0.13	0.64
GP/rabbit	owl	0.61	0.31	0.53	0.73	**0.00**
Interspecific predator comparisons						
GP	coyote/eg	0.85	0.22	0.06	0.13	0.08
GP	coyote/ov	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
GP	eagle/owl	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
rabbit	coyote/eg	0.50	0.38	0.85	1.00	0.31
rabbit	coyote/ov	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
rabbit	eagle/owl	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**

4.5. Bald eagles, great horned owls, coyotes, and other small prey accumulators

To determine the agents responsible for the accumulation of fossil bone, distinctive BSMs, fracture and breakage patterns, and prey skeletal-part representation of the potential accumulating agents must be identified. But distinguishing between the signatures of small mammal accumulators such as raptors, carnivores, and humans is challenging as there is often overlap among the taphonomic indicators as well as variability within accumulating agents; this may lessen as a wider variety of small mammal taphonomic studies become available. Appendix H provides a synopsis of current small mammal studies that

feature BSMs, fragmentation, and skeletal-part preservation data so as to compare the results of the present study with similar raptor and mammalian carnivore analyses. Unfortunately, the reporting of taphonomic information among small mammal studies is not standardized and the reporting of results is often inconsistent or incomplete. For instance, some studies report skeletal-part preservation frequencies of only select skeletal elements, while others report none at all. In other cases, BSMs such as punctures, pits, or digestion are reported simply as “present” or “absent” as opposed to specific counts of modification totals, and still others combine different types of BSMs and report only the combined totals. These inconsistencies make direct quantitative comparisons difficult. Therefore the following comparisons between the present study and similar studies summarized in Appendix H are broad and qualitative. In some cases comparisons could not be made due to lack of comparable information. Though quantitative comparisons are preferred, the comparisons discussed below are useful in characterizing taphonomic patterns within different groups of predators and between diverse prey taxa; all referenced comparisons in this section are in relation to the data presented in Appendix H.

Diurnal raptors: Neither the non-ingested or ingested portions of the BE-rabbit/GP samples closely resemble other diurnal raptor assemblages in terms of BSM frequencies, fragmentation, or skeletal-part representation. There are, however, some broad similarities (Appendix H). The BE-rabbit/GP samples generally feature fewer total BSMs (excluding digestion) in comparison to other

raptors. However, the BE-GP ingested sample total BSM frequency is similar to the golden eagle (Hockett, 1995) and prairie falcon (Hockett, 1995) leporid accumulations. The total fragmentation level of BE-rabbit/GP ingested samples are greater than the other diurnal raptor ingested samples while the non-ingested samples are roughly within the range of the other diurnal raptors degree of prey fragmentation. The skeletal-part profiles of the non-ingested and ingested portions of the BE-rabbit/GP samples do not closely match any of the other diurnal raptor assemblages. The skeletal-part profile differences are perhaps attributable to differences between assemblage origins: natural versus experimental accumulation of bone. Even when comparing the taphonomic profiles of taxa of similar size and build (i.e. rabbits to hares or GPs to *Bathyergus suillus*), the BE-rabbit/GP samples are largely dissimilar in relation to the other diurnal raptor assemblages. In fact, they are more similar to each other in terms of BSM and fragmentation frequency but feature very different skeletal-part preservation profiles.

Nocturnal raptors: The non-ingested and ingested GHO-rabbit/GP samples share more similarities with the other nocturnal raptor assemblages presented in Appendix H than the BE shares with the diurnal raptors. Total BSM frequencies and total fragmentation are similar between the GHO-rabbit sample and the corresponding nocturnal raptor assemblages. The skeletal-part profile of the GHO-rabbit ingested sample is comparable to Hockett's (1995) great horned owl and barn owl leporid ingested assemblages, though there are fewer hind limb

elements in the GHO-rabbit sample in comparison to these assemblages. Despite the size and build differences between GPs and leporids, the GHO-GP ingested sample shares some skeletal-part similarities with Hockett's (1995) great horned owl and barn owl ingested assemblages, particularly fore- and hind limb element abundances. However, the combined undigested and ingested Eurasia eagle-owl (Sanchis Serra, 2000; Lloveras et al, 2009) skeletal-part profiles are dissimilar to the GHO-rabbit/GP assemblages, which is surprising given their approximate similarities in size and prey preferences.

Carnivores: The non-ingested and ingested portions of the coyote-rabbit/GP samples are similar to a few other carnivore assemblages listed in Appendix H. The total BSM frequencies of the coyote-rabbit/GP samples are similar to the coyote (Schmitt and Juell, 1994) and to the Iberian lynx (Lloveras et al, 2008b; Rodríguez-Hidalgo et al., 2013b) assemblages; however, they are considerably less than the red fox leporid assemblages (Cochard, 2004; Lloveras et al, 2012). Total fragmentation among the coyote-rabbit/GP non-ingested and ingested samples are comparable to the coyote, red fox, and Iberian lynx leporid assemblages. This, despite the size and build differences between GPs and leporids. With regard to skeletal-part profiles, there are similarities between the coyote-rabbit ingested sample and the coyote leporid ingested (Schmitt and Juell, 1994) assemblage as well as between the coyote-GP ingested sample and the lynx-leporid ingested sample in terms of forelimb and axial element frequencies. However, there are differences in the abundance of hind limb

elements between each sample comparison. All other skeletal-part profile comparisons are dissimilar.

All told, the BE, GHO, and coyote assemblages presented in this paper share a mixture of similarities and differences with other diurnal and nocturnal raptors and carnivore taphonomic studies (Appendix H), but none are truly alike. The BE samples are generally different than other diurnal raptors in Appendix H, whereas the GHO samples share more taphonomic attributes with other nocturnal raptor studies. The coyote samples retain perhaps the most taphonomic similarities with several of the other carnivore (i.e. coyote and lynx) accumulations in comparison to what the raptors share with their respective groups.

It is not surprising that the BE-rabbit/GP samples have little in common with eagle-primate taphonomic studies (McGraw et al, 2006; Sanders et al, 2003; Trapani et al, 2006) as the size and body plan of the prey are quite different. It is reasonable to assume that disarticulation, consumption, and transport of primate prey differs from leporids or smaller prey like GPs given the role of prey size in relation to raptor consumption and transport documented by Armstrong and Avery (2014). It is surprising that the BE-rabbit samples do not share more taphonomic commonality with other diurnal raptor leporid samples given the similar size and build of the prey as well as the range of diurnal raptor leporid studies available for comparison. It seems that diurnal raptors (and specifically

eagles, Appendix H) display higher degrees of taphonomic variation (in terms of non-ingested- and fragmented-part profiles and BSMs) than other raptors even when only leporids are considered. As for the BE-GP sample, *B. suillus* accumulated by Verreaux's eagles is the published study featuring prey that most closely matches the size and build of GPs, but the study results share little in common. In fact, the BE-GP BSM frequency more closely matches golden eagle and prairie falcon leporid accumulations, again highlighting eagle taphonomic variability.

The lack of similarity between the diurnal raptor accumulations may also stem from the collections' origins. The controlled conditions and restricted space at the Raptor Center for the BE-rabbit/GP feeding samples -- as opposed to the collection of naturally accumulated prey remains of free-ranging raptors -- likely resulted in the greater recovery and representation of non-ingested and ingested bones in the BE-rabbit/GP samples. This contrast is reflected in the wildly different skeletal-part profiles between the BE-rabbit/GP and the diurnal raptor accumulations. There were considerably more skeletal elements recovered in the BE-rabbit/GP samples in comparison to other diurnal raptor assemblages (Appendix H). Another explanation of these differences may stem from the behaviors and adaptations of the birds corresponding to the adapted/expected food source. The disparity in BSMs between the samples may at least partially reflect the fact that the BE did not have to hunt its prey, so modifications that result from capture and transport may have been reduced.

The GHO- and coyote-rabbit/GP samples are more similar to their respective nocturnal raptor and carnivore assemblages than the BE is to the diurnal raptors. Between the two, the coyote samples are more similar to the other carnivore taphonomic studies (Appendix H) than the GHO samples are to the other nocturnal raptor accumulations. Like the BE-rabbit/GP samples, skeletal elements are more thoroughly represented in the GHO assemblage than in the other nocturnal raptor assemblages. The fact that Eurasian eagle-owl assemblages are combined non-ingested and ingested accumulations, but that the skeletal-part frequencies are far lower, corroborates the notion that bone collection via controlled feeding versus natural accumulation is at the root of the bone frequency differences. Nonetheless, the resemblance in digested skeletal-part profiles of the GHO samples and other great horned owl (Hockett, 1995) and barn owl digested assemblages may stem from the tendency of owls to minimize deletion of swallowed bone. With prey of a particular size and build, such as leporids, it is likely that particular bones such as forelimb and cranial elements are swallowed more often than others. This factor, coupled with the lack of bone deletion from digestion, is why in large part the nocturnal raptor digested samples share taphonomic profiles. Unfortunately, a non-ingested nocturnal raptor assemblage comparable to the GHO-GP prey size sample does not exist.

The taphonomic similarities between the digested portions of the coyote-rabbit/GP and the coyote (Schmitt and Juell, 1994) and lynx leporid samples likely derive from the feeding behavior of these predators. The skeletal-part

profiles, fragmentation totals, and the authors' observation of the coyote and raptor feeding, suggests that on average these carnivores consume, masticate, and digest many more prey bones than the raptors. Extensive consumption of the prey carcass occurred with both the rabbits and GP. The similarly low numbers of BSM frequencies likely result from substantial fragmentation and digestion of prey bones. BSMs, such as punctures and pits, probably do not survive extensive fragmentation and digestion. The relatively high incidents of BSMs observed in the non-ingested samples of *Vulpes vulpes* prey remains (Appendix H) attests to this observation.

5. CONCLUSIONS

This study provides a comprehensive taphonomic assessment of rabbits (3.8 kg average weight) and guinea pigs (1.4 kg average weight) accumulated by a bald eagle, great horned owl, and coyote under controlled conditions. The analysis includes both the ingested and non-ingested portions of the prey assemblages. The results reveal taphonomic differences between these diverse small mammal accumulators as well as variation between prey of different sizes. Small mammal actualistic and experimental taphonomic studies usually feature leporids as the prey species, however, this analysis – in addition to leporids – features guinea pigs, a prey taxon of different size and build, augmenting the range of actualistic and experimental small mammal taphonomic studies.

The results of this study indicate that there is considerable taphonomic variation between rabbits and guinea pigs modified by the bald eagle, great horned owl, and coyote. The predators produced significantly different intraspecific rabbit and guinea pig ingested and non-ingested skeletal- part profiles. The bald eagle and coyote produced significantly different intraspecific deleted-part profiles while the bald eagle and great horned owl generated significantly different intraspecific non-ingested fragmented-part profiles. In addition, the interspecific predator -part profile comparisons are, with few exceptions, dissimilar.

The intra- and interspecific predator BSM comparisons reveal a mixture of relationships underlining the differences between the predators and prey taxa. Some BSM frequencies are not significantly different, namely notch and score frequency. However, punctures, pits, digested, crenulated, and fractured edge specimens reveal a combination of significant and non-significant intra- and interspecific predator comparisons. In short, there are tangible BSM differences between the samples, further demonstrating that the predators handle small prey of different sizes and builds distinctively. Further, it is possible with the combined suite of BSM frequencies and -part profiles to distinguish between the prey samples by predator as demonstrated by the principal component analyses on BSM frequencies.

Taphonomic comparisons between this study and other diurnal raptor small mammal analyses reveal a high degree of variability in terms of ingested and non-ingested skeletal-part profiles, bone fragmentation, and BSM. It seems that different eagle taxa exhibit a wide range of taphonomic variation even when only leporids are considered. The great horned owl assemblages share more in common with other nocturnal raptor prey accumulations, particularly fragmentation and BSM frequency, and to a lesser extent skeletal-part frequencies. The coyote assemblages are taphonomically similar to other published coyote and Iberian lynx prey assemblages but surprisingly different than some fox accumulated leporid collections. Unfortunately there were very few assemblages to which the guinea pig samples could be compared; they were largely dissimilar to the leporid studies. All told, the comparisons reveal the range in variability but also the similarities among the small mammal taphonomic analyses, emphasizing the need for a wider assortment of small mammal predator and prey studies.

Based on this study, the implication for faunal analysts is that variability in small mammal assemblages is introduced by both predator and prey type. The taphonomic profile of leporids accumulated by a particular predator taxon may not match the profile of guinea pig-sized prey collected by the same predator. Therefore taphonomic patterns derived from predation on leporids by diurnal and nocturnal raptors and carnivores may not offer the appropriate proxies to identify predation on other prey taxa by these same predators. Expanding the base of

experimental and actualistic studies to included predation on non-leporid small mammals will help provide the proxies necessary to identify the origin of small mammal accumulations. Most archaeological assemblages feature a mixture of accumulators and analysis of raptor and carnivore predation on rabbits and guinea pigs presented in this study will help differentiate predation between these predators and humans in archaeological assemblages.

PROLOGUE (PAPERS 2 & 3)

Papers 1 and 2 provide the taphonomic control assemblages needed in order to accurately identify the accumulator(s) of small mammals at Die Kelders Cave 1 and Pinnacle Point site 5-6. Documenting and defining predation and consumption signatures for a variety of predators as well as different-sized prey is a critical component of this dissertation, especially as the taphonomic literature regarding small mammals, as well as prey assemblages available for study at museums and universities, are few and far between.

Paper 1 defines the patterns of preservation, breakage, and bone surface modification that can be employed on a taxon-specific basis to distinguish Verreaux's eagle prey remains from other bone accumulators and demonstrates that there is patterned variability in the ways that Verreaux's eagles accumulate and modify the bones of their prey.

Paper 2 provides an assessment of two small mammal taxa that differ in size and build and are broadly representative of small mammals recovered from archaeological sites. The study demonstrates that it is possible to distinguish between small mammal prey remains accumulated by diverse predators through the analysis of bone surface modifications, bone breakage patterns, and skeletal-part profiles.

Using the results of papers 1 and 2 – as well as analysis of the Dobe Base Camps forager assemblage – paper 3 looks to determine whether humans were

one of the chief accumulators of MSA small mammals at Die Kelders Cave 1 and Pinnacle Point site 5-6.

A total of 38,089 Die Kelders Cave 1 faunal specimens and 5,724 Pinnacle Point site 5-6 faunal specimens were identified and analyzed for bone surface modifications, bone breakage, and taxonomic and skeletal abundance. Each of the archaeofaunal samples was large and it was necessary to employ sampling strategies for portions of Die Kelders Cave 1 and for Pinnacle Point site 5-6; the samples obtained were sufficient to identify the bone accumulators and to identify accumulation patterns within the sites with a high degree of confidence. Within-site comparisons for patterns of bone surface modifications, bone breakage, and taxonomic composition were conducted. Principal component analyses were used to compare the bone surface modification profiles of the Die Kelders Cave 1 and Pinnacle Point site 5-6 assemblages with the profiles of the human, nocturnal and diurnal raptor, and mammalian carnivore assemblages of known accumulation described and analyzed in papers 1 and 2.

Paper 3 constitutes the first comprehensive taphonomic study of small mammals from South African MSA archaeological sites with direct and robust comparisons with control assemblages of known small mammal accumulation. Among the results is the first evidence for the habitual utilization of mole-rats and for the skinning of small, fur-bearing mammals during the MSA of South Africa, adaptive responses by MIS4 humans to glacial conditions and habitat

fluctuations that differ from behavioral adaptations exhibited during the previous glacial phase.

PAPER 3

Small mammal utilization by Middle Stone Age Humans at Die Kelders Cave 1 and Pinnacle Point Site 5-6, Western Cape Province, South Africa

SUMMARY

Reported here are the results of a taphonomic analysis of the small mammals (>.75 kg adult body weight) and size 1 bovids (≤20 kg adult body weight) from the Middle Stone Age (MSA) sites of Die Kelders Cave 1 (DK1) and Pinnacle Point Site 5-6 (PP5-6) located in the Western Cape Province, South Africa. This study provides the first comprehensive taphonomic analysis of MSA small mammals with a focus on discerning the role of humans in their accumulation and the implications for human behavioral adaptations in a region that features prominently in the investigation of modern human origins. Based on comparisons with control assemblages of known accumulation by humans, mammalian carnivores, and raptors (nocturnal and diurnal), it is evident that humans accumulated Cape dune mole-rats, hares, and size 1 bovids from throughout much of DK1. Nocturnal raptors also accumulated small mammals at DK1 and are the main accumulator in strata where anthropogenic input is minimal, a result consistent with previous zooarchaeological analysis at DK1. The patterning of cut-marked and burned Cape dune mole-rat remains at DK1 provides the first evidence in the MSA for the systematic utilization of small

mammals for their skins and as a protein source. Unlike DK1, small mammals and size 1 bovids constitute only a small portion of the PP5-6 mammals and they exhibit little evidence of human accumulation. Taphonomic indicators reveal that nocturnal and diurnal raptors accumulated most of the small mammals and size 1 bovids at PP5-6. The nominal presence of small mammals in the PP5-6 fauna is atypical of MSA sites in southern Africa's Cape Floristic Region, where small mammal taxa are abundant and often constitute large portions of MSA archaeofaunas.

With the assumption that the MSA occupation at DK1 dates to MIS4, DK1 humans maximized the environmental yield by exploiting low-quality resources, a strategy employed possibly in response to localized environmental conditions and to greater human population densities. In comparison, the MIS4 humans at PP5-6 did not exploit small mammals and instead focused on higher-quality resources like shellfish and large ungulates. Humans and predators did not accumulate small mammals in any substantial way at PP5-6, suggesting that these taxa may have been less abundant near the site and/or that humans could afford to concentrate exclusively on high-quality resources, perhaps because of a higher-yield local environment. Results of this study suggest that an adaptive response of humans to the environmental conditions of MIS4 was to maximize the resource yield of local habitats to include lower-quality resources when necessary. The incorporation of these resources in the face of changing environmental and population pressures is a subsistence adaptation that has not

been documented in the previous glacial phase of MIS6 and may have played a crucial role in the population stability and expansion evidenced by the substantial number of sites in the Cape dating to MIS4.

INTRODUCTION

There is general agreement that the African Middle Stone Age (MSA) began by ca. 285,000 years ago (Tryon and McBrearty, 2002; 2006) and persisted until ca. 30,000 years ago (Deacon and Deacon, 1999; McBrearty and Tryon, 2005; Tryon and McBrearty, 2006). Paleoanthropological and archaeological investigations of this time period are frequently rooted in questions concerning the origins of modern human behavior. Throughout Africa, archaeological sequences dating to the last half of the MSA have produced evidence for behavioral characteristics thought to be central to the expansion of modern humans out of Africa. There is consensus that these behaviors include the creation and use of symbols, technological and social complexity, and adaptable foraging strategies and use of landscapes (Barham, 2001; Brown et al, 2009; Brown et al, 2012; d'Errico et al, 2005; d'Errico et al, 2008; d'Errico et al, 2012; Deacon, 2001; Diez-Martín et al, 2009; Henshilwood, 2007; Henshilwood and Dubreuil, 2011; Henshilwood and Marean, 2003; Henshilwood et al, 2002; Henshilwood et al, 2009; Henshilwood et al 2011; Mackey and Welz, 2008; Marean, 2014; Marean et al, 2007; McBrearty and Brooks, 2000; McCall and

Thomas, 2012; Nash et al, 2013; Texier et al, 2010; Thompson and Henshilwood, 2014; Vanhaeren et al, 2013; Wadley, 2001; Wadley et al, 2011; Watts, 2010; Will et al, 2013; Wilkins et al, 2012; Wurz, 1999; Yellen and Brooks, 1995).

Recently, foraging strategies and landscape use in relation to modern human origins in southern Africa have received considerable attention (Clark, 2011; Clark and Kandel, 2013; Dusseldorp, 2010; 2012; Marean, 2014; Marean et al, 2014; Thompson, 2010a; Steele and Klein, 2009). The emphasis of this research has been the assessment (temporally and geographically) of purported changes in foraging strategies and landscape use as well as the analysis of subsistence adaptations that may have been driven by – or exhibited in – human behavioral changes during the MSA. While some research has considered small ungulate exploitation and time-saving technologies such as snares and traps (Wadley, 2010), much of this research has focused on the ability (Faith, 2008; 2011; 2013; Marean et al, 2000a; Milo, 1998; Thompson, 2010b; Thompson and Henshilwood, 2011) or inability (Binford, 1984; Klein, 1994; 1995; 1998; 2000; Klein and Cruz-Uribe, 1996; Weaver et al, 2011) of MSA humans to effectively and efficiently exploit large and sometimes dangerous ungulates.

In addition to the focus on large ungulate research, sessile and slow moving organisms have received increased scrutiny. Along the southern coast of South Africa, shellfish (Avery et al, 2008; Jerardino et al, 2014; Jerardino and

Marean, 2010; Klein et al, 2004; Langejans et al, 2012; Marean, 2014; Marean et al, 2007; Parkington, 2003; Steele and Klein, 2005/6; 2008) and tortoises (Avery et al, 2008; Henshilwood et al, 2001a; Klein et al, 2004; Klein and Cruz-Uribe, 1983; 2000; Steele and Klein, 2005/6; 2013; Thompson, 2010b; Thompson and Henshilwood, 2014a; 2014b) are often abundant at MSA sites and the study of their remains has addressed questions concerning human mobility patterns, paleodemography, prey choice, subsistence adaptations and foraging strategies.

With the increased scrutiny of MSA hunting and foraging adaptations as demonstrated by these and other studies, faunal analysts have redoubled their attention towards comprehensive taphonomic assessments of faunal remains, testing assumptions regarding the agents of faunal accumulation at southern African MSA archaeological sites and allowing for more comprehensive assessment of human foraging behaviors. This line of investigation has proven fruitful towards the attribution of agency and modes of human processing of large mammal archaeofaunas (Faith, 2013; Marean et al, 2000a; Milo, 1998; Thompson, 2010b; Thompson and Henshilwood, 2011) as well as tortoises (Steele and Klein, 2005/6; 2013; Thompson, 2010b; Thompson and Henshilwood, 2014a; 2014b) and shellfish (Jerardino et al, 2014; Jerardino and Marean, 2010; Langejans et al, 2012; Steele and Klein, 2008) by building on the extensive body of zooarchaeological studies from the MSA of southern African where the focus has previously been on taxonomic counts and individual body size comparisons.

However, with little exception (Badenhorst et al, 2014), small mammal MSA archaeofaunas have not received the same level of attention. This is somewhat puzzling as the Cape Floristic Region (CFR) currently and historically has supported a wide variety of small-bodied mammals (mole-rats, leporids, porcupine, rock hyrax, small carnivores, and others) and small-bodied ungulates (klipspringer, steenbok, and grysbok), many of which occur in large numbers at MSA archaeological sites (Blombos Cave, Boomplaas Cave, Die Kelders Cave 1, Diepkloof Rock Shelter, Ysterfontein 1, among others) in the Cape. This paper considers the small mammal (>.75 kg adult body weight) and size class 1 bovid (≤20 kg adult body weight) archaeofaunas from Die Kelders Cave 1 (DK1) and Pinnacle Point site 5-6 (PP5-6) and provides taphonomic analyses of their remains in order to evaluate the degree to which humans, raptors, and mammalian carnivores were involved in the accumulation of small mammals and size 1 bovids at these sites. This paper includes a detailed evaluation of human, raptor, and mammalian carnivore bone surface modification frequencies, bone breakage patterns, and comparisons of the DK1 and PP5-6 small mammal archaeofaunas with control assemblages of known human, raptor (diurnal and nocturnal), and mammalian carnivore accumulation. This taphonomic assessment allows for the evaluation of the role of small mammals in the resource base of humans at these sites and ─ together with large mammal, tortoise, and shellfish ─ for a more complete understanding of the range of

human subsistence strategies and foraging adaptations employed in the CFR during the MSA.

SITE DESCRIPTON – *Die Kelders Cave 1*

The Die Kelders Cave complex is located in the Walker Bay Nature Reserve ~120 km southeast of Cape Town and ~250 km west of Pinnacle Point site 5-6 (Fig. 23). The complex is situated ~10 m above mean sea level and is formed laterally between the contact of the Paleozoic quartzites of the Table Mountain Sandstone Group and the Cenozoic Bredasdorp Limestone Group (Tankard and Schweitzer, 1974). DK1 is a large locale adjacent to the unexcavated site of Die Kelders Cave 2. The site was originally excavated between 1969 and 1973 by Schweitzer and colleagues (Butzer, 1979; Schweitzer, 1970; 1974; 1979; Schweitzer and Scott, 1973; Tankard and Schweitzer, 1974; 1976), where the focus was on the Later Stone Age (LSA) component. It was then re-excavated between 1992 and 1995 by Avery, Marean, and colleagues (Avery et al, 1997; Goldberg, 2000; Marean et al, 2000b) with emphasis on the expansion of the Middle Stone Age aspect of the site.

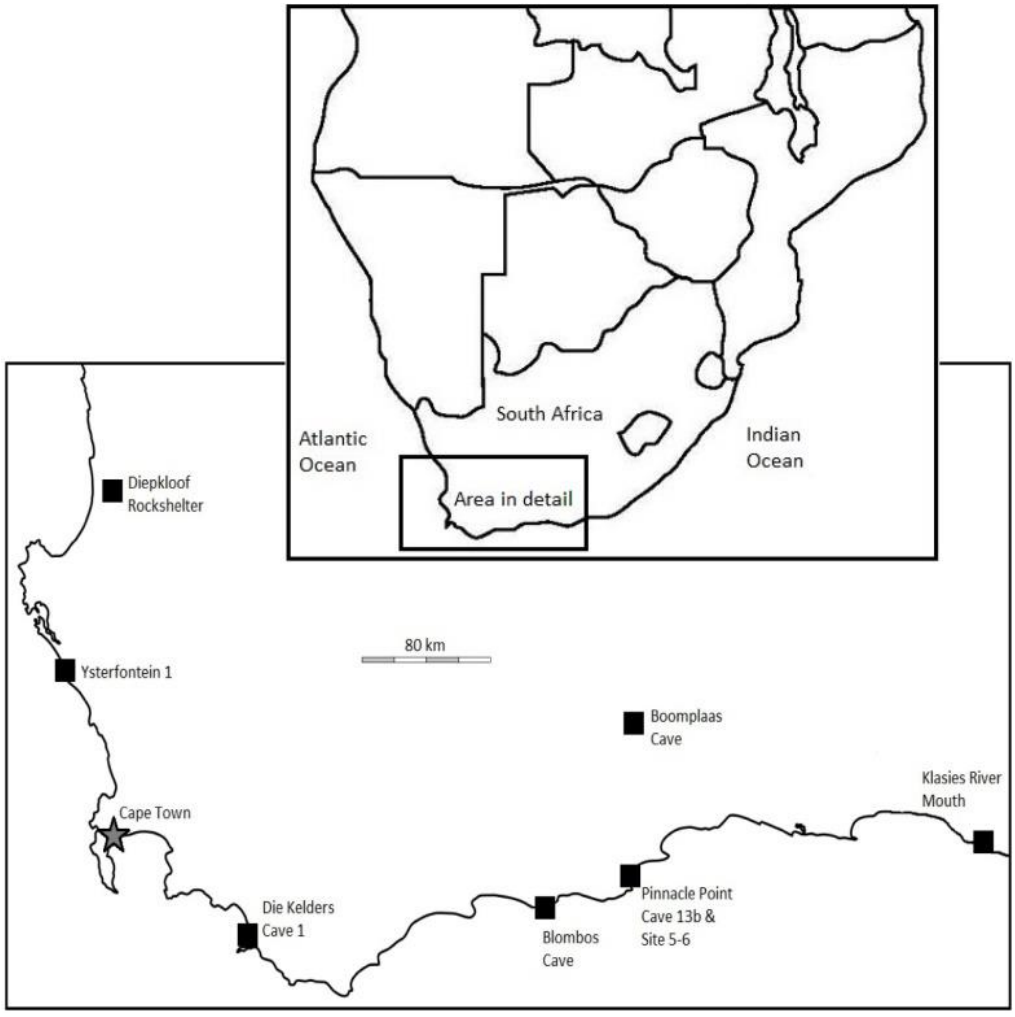


Figure 23: Locations of DK1, PP5-6, and other MSA sites discussed in the text.

DK1 is divided into 14 distinct stratigraphic layers; layers 1-3 were deposited during the LSA and layers 4/5-15 are recognized as MSA in origin (Marean et al, 2000b; Schweitzer, 1979). The sequence tends to alternate between layers of intense (even layers) and weak (odd layers) anthropogenic input (Marean et al, 2000b; Goldberg, 2000). For a complete description of the stratigraphy see Marean et al (2000b). The LSA occupation has been

radiocarbon dated to between 2000-1500 years BP (Schwietizer, 1974; 1979). The MSA sequence was dated with electron spin resonance (ESR; Schwarcz and Rink, 2000) and optically stimulated luminescence (OSL; Feathers and Bush, 2000) when these techniques were in the early stages of their application to cave sediments and therefore may not be as precise as the more recent versions of these dating techniques. Based on both original dating studies, age estimates for the MSA layers all fall within the error range of each other, making distinction of individual stratum ages unreliable. The consensus age estimate of the entire MSA sequence is ~70 ±10 ka BP based on the ESR (Schwarcz and Rink, 2000) and OSL (Feathers and Bush, 2000) studies. Further, luminescence dates obtained from throughout the MSA sequence suggest that the deposits accumulated fairly rapidly (Feathers and Bush, 2000) and faunal and sedimentological evidence further suggest that the entire MSA sequence was accumulated during a cool phase in Earth's climate, likely during marine isotope stage (MIS) 4 (71- 57 ka BP) (Avery et al, 1997; Goldberg, 2000; Grine et al, 1991, Klein and Cruz-Uribe, 2000). Given the cave's low elevation, deposits accumulated prior to MIS5e surely would have been washed away by the sea level high stand of the period. Based on consensus of dating techniques, fauna, sedimentology, and sea level, the assumption of this paper is that the MSA occupation of DK1 occurred during MIS4.

During the MIS4 human occupation at DK1 global sea level was between approximately -30 m and -80 m lower than present (Chappell and Shackleton,

1986; Lambeck, 2004; Lambeck and Chappell, 2001; Shackleton, 1987). Current estimates of coastline position during MIS4 indicate that it was nearly 17 km away at the beginning of the occupation and rose to within ~5 km by the end of the MSA occupation (Fisher et al, 2010; Hendey and Volman, 1986; Van Andel, 1989). This indicates that from the start to the end of the MSA occupation, the coastal geography of DK1 oscillated between a fully terrestrial to a near-coastal cave. However, the landscape in the immediate vicinity of DK1 likely remained relatively stable and can be characterized as a somewhat wetter environment featuring natural springs and streams and dominated by vegetated dune fields that included grasses (Goldberg, 2000; Klein and Cruz-Uribe, 2000; Marean et al, 2000b; Tankard and Schweitzer, 1974; 1976).

Marine mammals are moderately present throughout much the site, and complete marine shells are infrequently preserved in the MSA layers. However, Goldberg (2000) notes that shell fragments are common in micromorphology thin sections and that the absence of well-preserved shell is due to decalcification as opposed to strictly the lack of exploitation by humans. Marine mammals are present in proportions of between 1-13% by NISP throughout the MSA sequence (except for layers 7 and 8 where there are none; Klein and Cruz-Uribe, 2000). There is consistent ethnographic (Bird and Bliege Bird, 1997; Bird et al, 2002; Thomas, 2002) and archaeological (Erlandson, 2001; Jerardino, 2003; Langejans et al, 2012; Marean, 2014; Parkington et al, 1988) evidence to suggest that humans transport shellfish back to residential sites when the distance from the

shore does not exceed 10 km. The presence of marine resources at DK1 and current estimates of coastline position during MIS4 suggests that the coastline was likely no more than 10 km from the cave for much of the MSA occupation. However, given the degraded state and lack of complete sea shells as well as modest numbers of marine mammal bone, it seems that MSA humans at DK1 did not extensively rely on marine resources.

The lithic component of DK1 is composed mostly of course grained quartzite and some fine grained silcrete (Thackeray, 2000). Though the segments and backed-blades diagnostic of the Howiesons Poort (HP) are absent from the site, there is a shift from course to fine grained raw material in MSA layer 12, a pattern typical of southern African MSA sites that feature HP levels (Brown, 1999; Thackeray, 2000). However, definite assignment of the DK1 lithic material to a recognized MSA typology is precluded given the absence of HP (and Still Bay) and the tendency of southern African MSA artefact assemblages to lack distinct patterning outside of these industries (Thackeray, 2000).

The DK1 fossil component features a diverse and large assemblage that includes mammals, reptiles, birds, and hominins (Avery et al, 1997; Klein and Cruz-Uribe, 2000; Grine, 2000). The micromammals (<750 g adult body weight; Avery, 1982), macromammals (>750g adult body weight; Klein and Cruz-Uribe, 2000), and tortoises (Klein and Cruz-Uribe, 2000) have been analyzed for taxonomic abundance and paleoenvironmental interpretation. On the whole, the

faunal assemblage is dominated by small mammals (those between 0.75 kg and 4.5 kg body weight) that account for the overwhelming majority of the assemblage (>85%; Klein and Cruz-Uribe, 2000), most of which are Cape dune mole-rats (*Bathyergus suillus*; Table 1). The ungulates predominantly consist of smaller-bodied (e.g. *Raphicerus sp.*) and larger-bodied bovids (e.g. *Taurotragus oryx*). The taxonomic composition of the LSA fauna suggests that environmental conditions during the LSA occupation were similar to those of today (Klein and Cruz-Uribe, 2000). The MSA faunal composition features species historically associated with the CFR as well as extralimital (i.e. quagga, black wildebeest, springbok, and southern reedbuck) taxa (Klein and Cruz-Uribe, 2000). The presence of both extant and extralimital species as well as arid-adapted (e.g. black wildebeest, blue antelope, and springbok), water-dependent (e.g. hippopotamus, grey rhebok, and southern reedbuck), and taxa associated with open grassy habitats (e.g. eland and hare) signifies that environs in close proximity to DK1 were different than today, and appear to have included a mixture of closed and grassy habitats (Avery, 1982; Klein and Cruz-Uribe, 2000; Marean et al, 2000a). The MSA faunal composition of DK1 indicates that the cave was situated near relatively diverse ecological habitats (Marean et al, 2000a).

Taphonomic analyses of ungulates and marine mammals from MSA layers 9-15 have been conducted (Marean et al, 2000a; Thompson, 2008) and results from layers 10-11 have been published (Marean et al, 2000a). Overall,

the bone surface preservation of mammals can be characterized as very good (Marean et al, 2000a and personal observation). The analyses by Marean and colleagues (2000a) and Thompson (2008) indicate that the larger mammals (particularly size 2-5 ungulates) were principally accumulated by MSA humans. Numerous percussion, filleting, and disarticulation marks on ungulate bones are the primary evidence for human agency. Some of the size 1 bovid remains displayed evidence of human accumulation in the forms of cut and percussion marks. However, many size 1 bovid bones exhibited gastric etching which Marean et al (2000a) attributed to raptors, an observation supported by Klein and Cruz-Uribe (2000). Furthermore, Klein and Cruz-Uribe (2000) observed that many of small bovid individuals are juveniles, a prey demographic pattern associated with raptor predation (Avery, 1990). Overall, the occurrence of carnivore tooth-marked bone is moderate to low, indicating minimal levels of carnivore involvement in ungulate bone accumulation. Marean et al (2000a) ascribed the carnivore tooth marks to scavengers who occasionally and intermittently occupied the site when humans were not present.

DK1 small mammal investigation

The small mammal component of DK1 has not previously been taphonomically studied. However, Klein and Cruz-Uribe (2000) supposed that the MSA small mammal accumulation (particularly the Cape dune mole-rats) was

likely the result of predators but did not rule out the possibility of some human agency. They reasoned that Cape eagle-owls (*Bubo capensis*) probably accumulated the MSA mole-rats (and implicitly other small mammals) based on three factors: (1) mole-rat remains were unusually abundant (accounting for 90% of the fauna by MNI in some areas of the site and reaching a density of 100 individuals per square meter in the middle of MSA layer 8), (2) mole-rat skeletal-part profiles resembled eagle-owl prey patterning, and (3) some mole-rat remains appeared digested. In addition, the predatory behavior of the Cape eagle-owl, namely the owl's tendency to focus on colonial species, roost in caves and rockshelters (often on the floor), and its ability to transport animals >1.5 kg in weight (Avery, 1990) implicate the Cape eagle-owl as the principal candidate for small mammal accumulation. However, Klein and Cruz-Uribe's (2000) observations were macroscopic, largely impressionistic, and the mole-rat skeletal part frequencies, digested bone frequencies, and affected anatomical-part distributions were not quantified and reported. Another line of evidence to suggest that raptors may have been involved in the accumulation of bone at DK1 is Marean et al's (2000a) observation that some of the size 1 bovid remains display digestion damage (particularly podial elements) typical of raptors.

Additionally, Klein and Cruz-Uribe (2000) note that it is conceivable that mammalian carnivores and/or humans could have been involved in the accumulation of small mammals but that the assemblage was not studied taphonomically and that their overall assessment of small mammal accumulation

is somewhat provisional. They go on to suggest that "a damage analysis would be particularly telling if it revealed etching by eagle owl gastric acids . . . most etching might be visible only under very high magnification . . . a thorough microscope study would probably require many months (Klein and Cruz-Uribe, 2000: p.188)." Conversely, Klein and Cruz-Uribe (2000) concluded that humans played a role in the accumulation of LSA small mammals (including mole-rats) as "obviously burnt or cutmarked specimens occur only in the LSA assemblage (p.188)." Unfortunately, these macroscopic observations were not quantified and the surface modification patterns were not reported. They provide further evidence to support a LSA and MSA contrast in small mammal accumulation in noting that the mole-rat-rich LSA microstratigraphic layers tend to contain bones of many other taxa while mole-rat-rich MSA layers often contain bones of little else which suggest a single (non-human) predator specializing on a lone prey species.

SITE DESCRIPTION – PP5-6

Pinnacle Point site 5-6 is a rockshelter situated in wave-cut Paleozoic quartzitic cliffs of the Table Mountain Sandstone Group and is located ~6 km west of Mossel Bay on a southward oriented promontory facing the Indian Ocean (Fig. 23). The site is divided into three areas: the Northwest Remnant, the Long Section, and the South Remnant (Karkanas et al, 2015). The main

archaeological sequence is the Long Section which is exposed by a continuous >14 m vertically excavated profile of MSA deposit (Brown et al, 2012; Karkanas et al, 2015). The northern and southern ends of the Long Section are ~25 m and ~16 m above mean sea level respectively (Brown et al, 2012). The archaeological sequence consists of 11 horizontally continuous stratigraphic aggregates each representing major changes in anthropogenic and geogenic sedimentary inputs (Karkanas et al, 2015). The MSA basal deposit likely began accumulating prior to MIS5b (Brown, 2011); OSL samples at the top and near the bottom of the excavated profile have yielded dates of 51 ±2 ka BP and 96 ±6 ka BP respectively (Karkanas et al, 2015). There is no LSA in the main PP5-6 deposit. For a detailed discussion of the stratigraphy and ages see Karkanas et al (2015).

The paleoenvironmental and paleoclimate context for the PP5-6 archaeological sequence are inferred from speleothem-based carbon and oxygen isotope records (Bar-Matthews et al, 2010). Overlapping speleothem samples dating from 53 to 90 ka BP (uranium-thorium) were retrieved from a cave neighboring PP5-6. These high-resolution records, contemporaneous with the MSA occupation of PP5-6, show that Pinnacle Point and the surrounding environ changed rapidly during the period of human occupation. The late MIS5 period is typified by shrubby CFR (fynbos) vegetation and C3 grasses as well as increased winter rainfall. The cooler conditions of MIS4 are characterized by an increase in C4 grasses and more summer rainfall in the region. The speleothem

record further records a global climate excursion at ~72 ka BP (possibly the Toba eruption) which appears to have resulted in highly unpredictable local climate and environmental conditions around this interlude (Bar-Matthews et al, 2010).

In conjunction with the terrestrial-based carbon and oxygen isotope records, Fisher et al (2010) developed a three dimensional GIS-based sea level curve for the southern African coastline that integrates the topography of the submerged Agulhas Bank and the sea cliffs at Pinnacle Point and provides estimates of coastline position at 1500-year intervals. During warmer periods in global climate, such as the late MIS5 occupation, PP5-6 was a coastal cave similar to today where inhabitants relied on CFR and marine resources, indicated by the shell deposits dated to this period (Karkanas et al, 2015). During the cooler phase of MIS4, PP5-6 was an inland cave located between ~10-20 km from the coastline on average (Fisher et al, 2010). The site would have overlooked grassy plains that supported large ungulates but still offered access to the coastline and its resources. At this time there is a shift to microlith technology at PP5-6, which may have been used as armaments for large mammal hunting (Brown et al, 2012), suggesting the increased importance of large game during this period (Karkanas et al, 2015).

The MSA deposit at PP5-6 features abundant fauna, lithics, ochre, ostrich eggshell, and combustion features (Karkanas et al, 2015). To date, only the lithics (Brown, 2011; Brown et al, 2009; 2012), site formation processes, and

occupation intensity (Karkanas et al, 2015) have been extensively reported. Similar to other South African coastal MSA sites, PP5-6 demonstrates a transition from course grained quartzite to finer grained silcrete. The HP is present at PP5-6 (Brown et al, 2012) at an age consistent with other HP occurrences in southern Africa, ~65-60 ka BP (Jacobs et al, 2008a). In addition, Brown and colleges (2012) have reported a previously unidentified microlithic backed 'bladelet' technology that differs in form from microlithic HP segments. This distinctive PP5-6 'bladelet' technology appears ~6000 years prior to the HP, thereby representing an early origin for microlithic technology in southern Africa. In addition, Brown et al (2009; 2012) demonstrate that heat treatment of lithic raw materials was integral to the microlith production sequence and that this technological innovation persisted for nearly 100 ky. Brown et al's research suggests that complex lithic technologies in southern Africa occurred both earlier and lasted longer than previously thought.

The geoarchaeological analysis reported by Karkanas and colleges (2015) details the patterns of anthropogenic and geogenic input throughout the MSA occupation of PP5-6. Coarse and fine grained analyses of the sediments have revealed differences between the MIS5 and MIS4 human occupation patterns of the site. During MIS5 the coastline was close to the site and it appears that small groups of people were exploiting coastal resources and visiting the locale for short periods of time as evidenced by parts of the sequence that are characterized by numerous single hearth structures (Karkanas et al, 2015). With

the beginning of MIS4, occupations became much more intense as evidenced by thick palimpsests of burned anthropogenic materials and the presence of aggregated combustion features. During this time the inhabitants shifted to silcrete as a preferred raw material and began to make microlithic tools (Brown et al, 2012; Karkanas et al, 2015). Based on their study of PP5-6 and the abundance of sites dating to MIS4 in the region, Karkanas and colleges suggest that human populations in the Cape adapted to the cooler climate through technological change and population growth or stability and that the response of MIS4 humans was different to that of the previous glacial phase.

MATERIALS AND METHODS

The DK1 and PP5-6 faunal samples reported here are limited to mammalian specimens between 0.75 kg – ~4.5 kg adult body weight and Brain's (1974) size class 1 bovids. Though typically >4.5 kg, size 1 bovids have been included in the study samples as the suite of predators (raptors, carnivores, and humans) that commonly prey on small mammals also frequently target and accumulate size 1 bovids (Armstrong and Avery, 2014; Avery et al, 1987; Yellen, 1991a). In addition, digested size 1 bovid remains (particularly *Raphicerus sp*.) attributed to raptor accumulation were identified in the MSA fauna at DK1 (Marean et al, 2000a) and their relative frequencies in relation to other small fauna may provide evidence of the extent of raptor contribution in specific

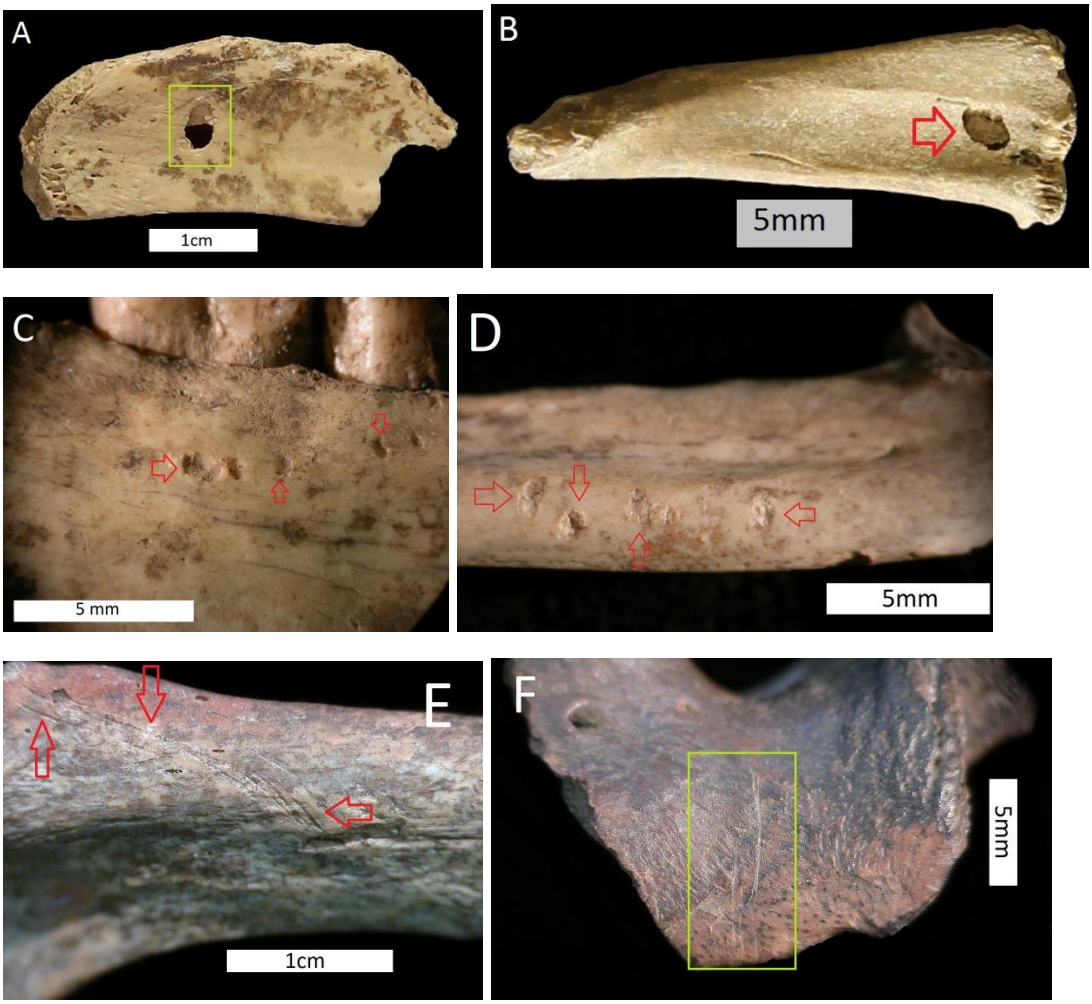
stratigraphic layers and the site as a whole. For the purpose of simplicity and succinctness within the context of this paper, the term small mammal will include specimens between 0.75 kg – ~4.5 kg as well as size 1 bovids unless otherwise stated.

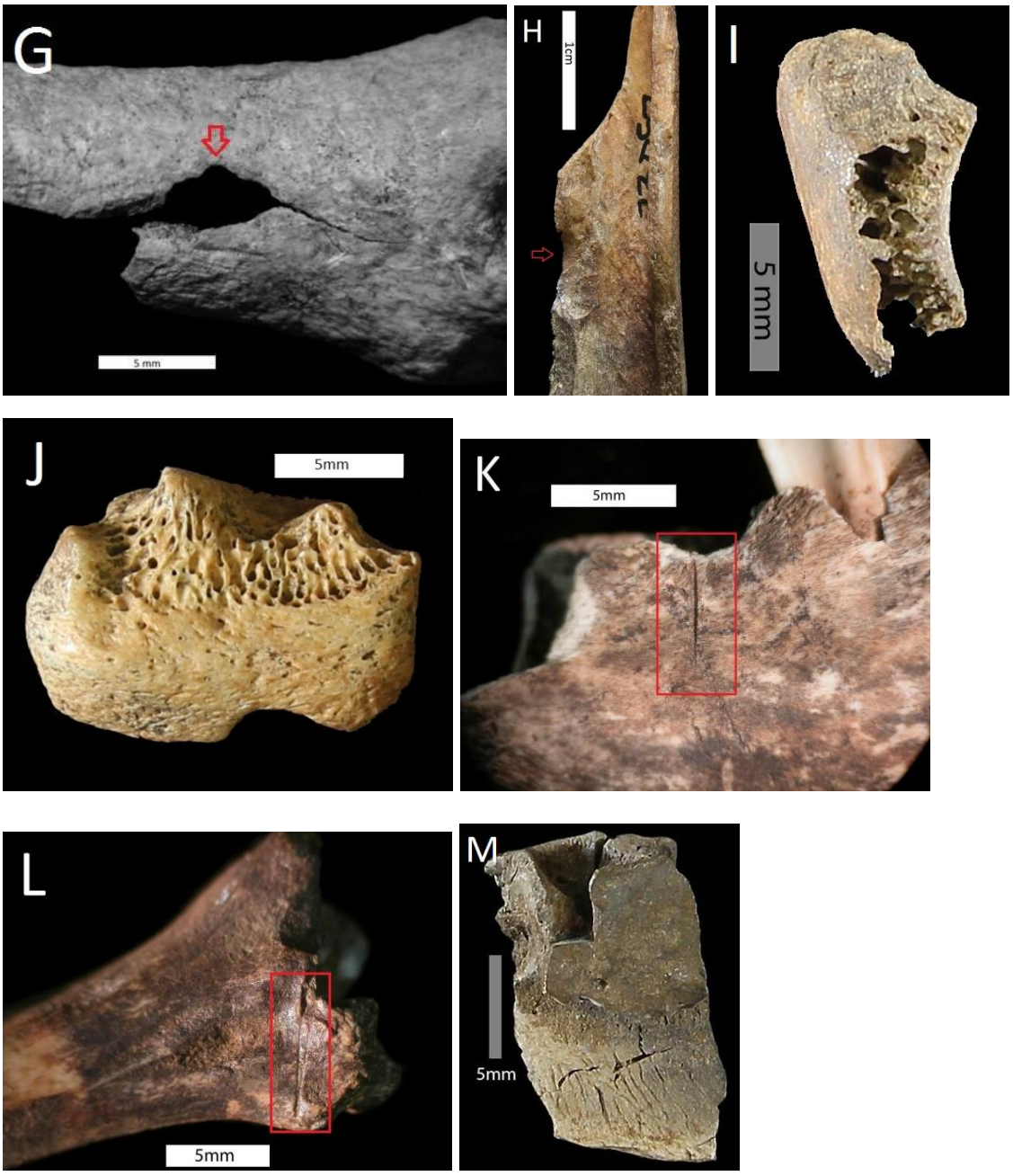
The portion of preserved bone, orientation of paired elements, and taxon were identified and recorded for each specimen. An attempt was made to identify each specimen regardless of size. Most specimens could be identified to a specific skeletal element, however some fragmentary specimens lacked diagnostic features and were identified as vertebra fragment, long bone shaft fragment, tooth fragment, or unidentifiable fragment >2 mm. Bone fragments that were unidentifiable and <2 mm in maximum dimension were excluded from the analysis. The maximum length and width of each specimen was measured using digital calipers. Comparative zoology collections from the Iziko Museum in Cape Town and the Diaz Museum in Mossel Bay were used in the specimen identification process.

All specimens were inspected with a 10-40x binocular zoom microscope under high incident light to examine for and document bone modifications using previously established criteria (Blumenschine et al, 1996). Digestive alteration to teeth and bones was observed and recorded after Andrews (1990) and summarized according to Lloveras et al (2008a). The presence or absence of burning was observed and characterized based on color variation ranging from

absent to complete calcination (Stiner et al, 1995). Taphonomic attributes such as rodent gnawing, weathering (for small mammal remains [Andrews, 1990]), and post-depositional surface destruction (Thompson, 2005) were observed and their anatomical location was recorded. The characterization, frequency, and location of mammalian carnivore, raptor, and human induced punctures (Andrews, 1990; Binford, 1981; Blumenschine et al., 1996; Brain, 1981; Elkin and Mondini, 2001; Hockett, 1991, 1995; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al. 2007; Sanders et al., 2003; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014a; Trapani et al., 2006), pits (Binford, 1981; Blumenschine and Selvaggio, 1988; Blumenschine et al., 1996; Domínguez-Rodrigo and Piqueras, 2003; Domínguez-Rodrigo et al., 2013; Elkin and Mondini, 2001; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al. 2007; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014a), scores (Binford, 1981; Blumenschine et al., 1996; Bunn, 1981; Elkin and Mondini, 2001; Haynes, 1980; 1982; 1983; Landt, 2007; Lyman, 1994; McGraw et al., 2006; Pickering and Wallis, 1997; Pobiner et al., 2007; Sanders et al., 2003; Shipman, 1981; Shipman and Rose, 1983; Tappen and Wrangham, 2000; Thompson and Henshilwood, 2014a; Trapani et al., 2006), notches (Binford, 1981; Blumenschine and Selvaggio, 1991; Brain, 1981; Capaldo and Blumenschine, 1994; Domínguez-Rodrigo et al., 2013; Fisher, 1995; Haynes, 1982; Landt, 2007; Pickering and Wallis, 1997; Pobiner et al., 2007), and cut marks (Binford, 1981; Blumenschine et al, 1996; Cochard et al, 2012;

Domínguez-Rodrigo and Barba, 2005; Domínguez-Rodrigo and Yravedra, 2009; Domínguez-Rodrigo et al, 2009; Egeland, 2003; Fernández-Jalvo et al, 1999; Gifford-Gonzalez, 1989; Lupo and O'Connell, 2002; Potts and Shipman, 1981; Shipman, 1983) were recorded using criteria adopted from established sources in the taphonomic literature. Examples of the bone surface modification documented in this study can be found in Fig. 24.

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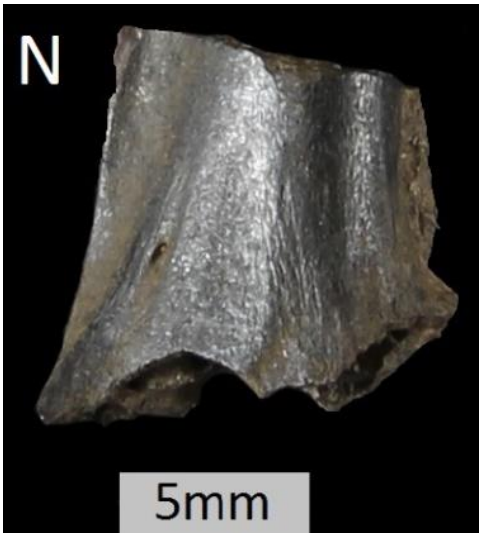


Figure 24A-N: Examples of the bone surface modifications described in this study: A-B=punctured mole-rat ilium and tibia; C-D=pitted rock hyrax mandible and mole-rat ulna; E-F=scored hare tibia and mole-rat mandible; G-H=notched bovid tibia and long bone shaft fragment; I-J=digested mole-rat patella and bovid fibula; K-L=cut-marked mole-rat mandible and tibia; M-N=burned hare femur and mole-rat humerus.

Long bone breakage concerning the morphology of fracture angle and fracture outline was recorded following Villa and Mahieu (1991). Fragmentation indices and whole bone percentages were calculated for each skeletal element by dividing NISP by MNE and whole bones by NISP, respectively.

The DK1 small mammal faunal sample included in this study consists of specimens excavated by Schweitzer and by Avery, Marean, and colleges. Given the enormous quantity of faunal remains from DK1, it was necessary to sample the largest excavation layers; these include the LSA and MSA layers 6-8. The faunas from layers 9-15 are less numerous, therefore it was possible to study

each specimen, including the wet-sieved materials. MSA layer 4/5 was excluded from study due to substantial stratigraphic mixing in relation to large quantities of fallen roof blocks and debris as well as the overall time constraints of the project.

The fauna from DK1 were not piece-plotted. Excavation was conducted along natural micro-stratigraphic units for each 1 m excavation square and faunal specimens were associated with individual micro-stratigraphic units (Marean et al, 2000b). Typically, there were multiple micro-stratigraphic units per 1 m excavation square and stratigraphic layer. For the sampled layers (LSA and MSA 6-8), a minimum of 200 specimens were studied from each of the 1 m excavation squares (unless the square yielded a total of <200 small mammal specimens) per layer. Between both phases of the excavation, there were 72 excavation squares in MSA layer 6, 52 in MSA layer 7, and 53 in MSA layer 8. The faunal sample from each 1 m square was randomly selected and all small mammal specimens (including wet-sieved materials) from selected micro-stratigraphic units were studied regardless of count total. In many cases, the count far exceeded the 200 specimen minimum per excavation square per layer. Where there were fewer than 200 specimens in a micro-stratigraphic unit, an additional micro-stratigraphic unit from the same square and layer was selected for study in order to achieve ≥200 specimens per excavation square. Studying all small mammal specimens from a micro-stratigraphic unit in each excavation square allows for a robust sample, relative skeletal-part analysis, and examination of horizontal spatial patterning within and between layers. In total,

3912 LSA, 8496 MSA layer 6, 5890 MSA layer 7, and 9075 MSA layer 8 small mammal specimens were studied.

The PP5-6 small mammal faunal assemblage consists of specimens excavated during the 2006-2010 excavation seasons. All specimens in this study were piece-plotted or recovered from the wet-screened materials associated with specific stratigraphic units and proveniences. The site's stratigraphic aggregates consist of numerous horizontally bedded sub-aggregates in which there are multiple micro-stratigraphic units associated with each 1 m excavation square. In order to achieve a faunal sample that was temporally and spatially representative, unbiased, and robust, the fauna from several micro-stratigraphic units from each sub-aggregate were randomly selected for study. A minimum of one micro-stratigraphic unit for every 10 was selected for study; the only condition for selection was that the unit contained fauna. In all, 115 micro-stratigraphic units were sampled. As the fauna from PP5-6 had not been previously studied, the proportion of small to large mammalian fauna and the stratigraphic location of small mammal specimens were not known. Therefore it was necessary to identify all randomly selected faunal materials. Of the 5724 faunal specimens sampled only 208 were small mammals. Figure 3 depicts the spatial distribution of all sampled faunal specimens (Fig. 25A) and the location of the identified small mammals (Fig. 25B) in relation to the stratigraphic aggregates.

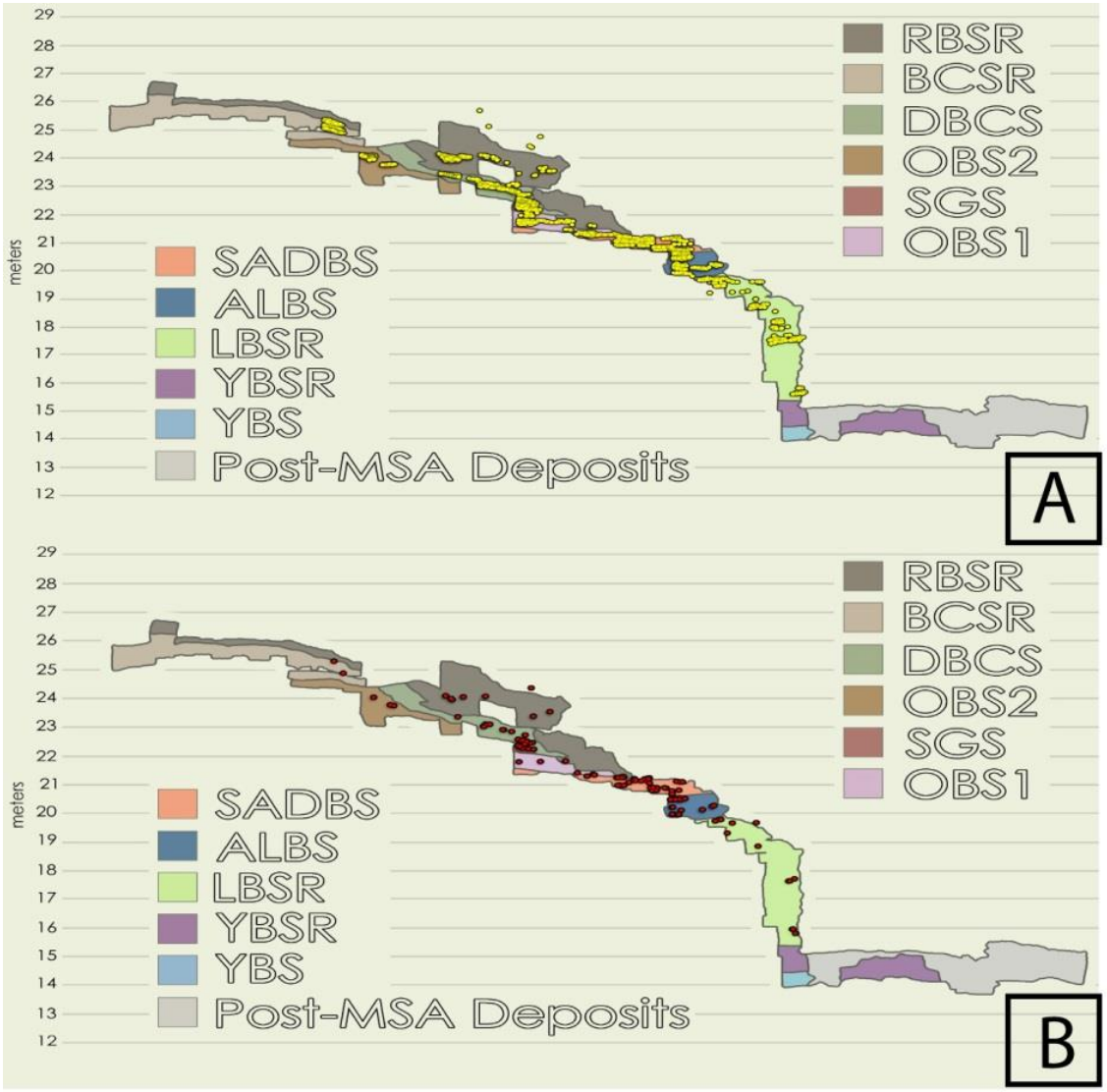


Figure 25: (A) Depiction of the PP5-6 Long Section and the locations of all sampled faunal specimens in relation to the stratigraphic aggregates. (B) Locations of the identified small mammal specimens. Stratigraphic aggregate ages (thousand years BP): RBSR 51 ±2, BCSR 52 ±3, DBCS 62 ±3, OBS2 63 ±3, SGS 64±3, OBS1 69 ±3, SADBS 71 ±3, ALBS 72 ±3, LBSR 81 ±4, YBSR 89 ±5, YBS 96 ±6.

RESULTS AND ANALYSIS

DK1 – Taxonomic composition

The taxonomic composition and specimen counts of all mammals >0.75 kg from DK1 have been reported previously by Klein and Cruz-Uribe (2000). Table 20 represents the DK1 faunal sample described in this paper and is in agreement with the identified small mammal taxa and counts reported by Klein and Cruz-Uribe (2000). For analytical purposes, the DK1 sample has been aggregated into five analytical units based on the taxonomic composition, morphological similarities, and relative abundance. The small mammal analytical aggregates (SMA) are: (1) mole-rats (consisting of only *B. suillus*), (2) size 1 bovids (all specimens identified to *Raphicerus* spp., *R. melanotis, R. campestris, O. oreotragus*, and size 1 bovid), (3) hares (all specimens identified to *Lepus* spp., *L. capensis,* and *L. saxatilis*), (4) rock hyraxes (consisting of only *P. capensis*), and (5) small carnivores (consisting of all herpestids, felids, mustelids, erinaceids, and viverrids). The relative proportions of the SMAs by level are reported in Table 1. Mole-rats are the dominant taxon by NISP in all but one level at DK1. Size 1 bovids, followed by hares, are the next two most numerous taxonomic aggregates, followed by rock hyraxes and small carnivores, each of which are noticeably less abundant than the other SMAs.

Table 20: Taxonomic representation by NISP of each identified taxon and analytical aggregate by stratigraphic layer for the DK1 sample.

Table 20: Taxonomic representation by NISP of each identified taxon and analytical aggregate by stratigraphic layer for the DK1 sample.

Taxa	Vernacular names	LSA	%	MSA6	%	MSA7	%	MSA8	%	MSA9	%	MSA1	%	MSA1	%	MSA1	%	MSA1	%	Total	%
Bathyergus suillus	Cape dune mole-rat	2810	71.83	4058	47.76	5622	95.45	8952	98.64	4063	90.83	1520	74.58	368	59.84	457	57.13	284	58.08	460	22.07	109	48.23	28703	75.34
Lepus spp.	Hares	23	0.59	1789	21.06	98	1.66	56	0.62	129	2.88	95	4.66	15	2.44	54	6.75	50	10.22	749	35.94	48	21.24	3106	8.15
Procavia capensis	Rock hyrax	295	7.54	171	2.01	9	0.15	6	0.07	54	1.21	57	2.80	7	1.14	55	6.88	19	3.89	119	5.71	10	4.42	802	2.11
Hystrix africaeaustralis	Porcupine	7	0.18							2	0.04													9	0.02
Atelerix frontalis	Hedgehog			5	0.06															2	0.10			7	0.02
Mellivora capensis	Honey badger	3	0.08	1	0.01	2	0.03			1	0.02					2	0.41							9	0.02
Genetta spp.	Genet	27	0.69	4	0.05	1	0.02									2	0.41							34	0.09
Galerella pulverulenta	Cape grey mongoose	16	0.41	17	0.20							1	0.05			7	0.88			28	1.34			69	0.18
Mongoose indet	Mongoose			12	0.14																			12	0.03
Felis silvestris lybica	Wildcat	11	0.28	9	0.11											1	0.13	1	0.20	1	0.05			23	0.06
Caracal caracal	Caracal	8	0.20							2	0.04									1	0.05			11	0.03
Canis mesomelas	Black-backed jackal	1	0.03					1	0.01			3	0.15					2	0.41					7	0.02
Vulpes chama	Cape fox	7	0.18																					7	0.02
Ictonyx striatus	Striped polecat	41	1.05									1	0.05							3	0.14			45	0.12
Oreotragus oreotragus	Klipspringer			2	0.02	1	0.02			1	0.02			1	0.16					3	0.14	2	0.88	10	0.03
Raphicerus spp.	Grysbok / steenbok	238	6.08	454	5.34	16	0.27	11	0.12	35	0.78	95	4.66	13	2.11	58	7.25	23	4.70	214	10.27	2	0.88	1159	3.04
	Size 1 bovid	425	10.86	1974	23.23	141	2.39	49	0.54	186	4.16	266	13.05	211	34.31	168	21.00	106	21.68	504	24.18	55	24.34	4085	10.72
	Total	3912		8496		5890		9075		4473		2038		615		800		489		2084		226		38098	
	Analytical Aggregates																								
	Mole-rats	2810	71.96	4058	47.76	5622	95.45	8952	98.64	4063	90.87	1520	74.58	368	59.84	457	57.13	284	58.08	460	22.07	109	48.23	28703	75.36
	Hares	23	0.59	1789	21.06	98	1.66	56	0.62	129	2.89	95	4.66	15	2.44	54	6.75	50	10.22	749	35.94	48	21.24	3106	8.15
	Hyraxes	295	7.55	171	2.01	9	0.15	6	0.07	54	1.21	57	2.80	7	1.14	55	6.88	19	3.89	119	5.71	10	4.42	802	2.11
	Carnivores	114	2.92	48	0.56	3	0.05	1	0.01	3	0.07	5	0.25	0	0.00	8	1.00	7	1.43	35	1.68	0	0.00	224	0.59
	Size 1 bovids	663	16.98	2430	28.60	158	2.68	60	0.66	222	4.97	361	17.71	225	36.59	226	28.25	129	26.38	721	34.60	59	26.11	5254	13.79
	Total	3905		8496		5890		9075		4471		2038		615		800		489		2084		226		38089	

At DK1, mole-rats are numerous in relation to all mammals throughout the site representing a total of 75.3% by NISP of all specimens in this study, and account for >90% of all specimens in MSA layers 7-9 at DK1. For comparison, mole-rats account for 93.2%, 31.3%, 31.9%, and 0.0% by NISP of all small mammals at Ysterfontein 1 (YFT1; Avery et al, 2008), Blombos Cave (BBC; Henshilwood et al, 2001a), Diepkloof Rockshelter (DRS; Steele and Klein, 2013), and Pinnacle Point 13b (PP13b; Thompson, 2010b), respectively. However, at DK1 the proportion by NISP of Cape dune mole-rats to other small mammals varies per stratum (LSA = 71.8%, MSA6 = 47.8%, MSA7 = 95.4%, MSA8 = 98.6%, MSA9 = 90.8%, MSA10 = 74.6%, MSA11 = 59.8%, MSA12 = 57.1%, MSA13 = 58.1%, MSA14 = 22.1%, MSA15 = 48.2%), and though the frequency of mole-rats as a percentage of all small fauna decreases from more recent to older layers, the correlation is not significant ($r^2 = 0.336$, $p = 0.062$). It is clear, however, that mole-rats are abundant in all layers and super abundant in layers MSA7-9, but that their relative frequency varies over time.

Of the MSA sites in the CFR for which taxonomic abundances of small and large mammals are reported, YFT1 (Avery et al, 2008; Halkett et al, 2003; Klein et al, 2004), BBC (Thompson and Henshilwood, 2011; Henshilwood et al, 2001a), and DRS (Steele and Klein, 2013) are more similar to DK1 in terms of small and large mammal relative abundances. Conversely, PP13b differs from DK1 as there are few small mammals in relation to large (Rector and Reed, 2010; Thompson, 2010b). Taxa such as Cape dune mole-rats, rock hyrax, hare,

and small carnivores are far more common at DK1, YFT1, BBC, and DRS in comparison to PP13b. In addition, Thompson and Henshilwood (2014) observed that tortoise representation similarly varies in frequency between these sites. They also note that in the CFR, it is the more “typical” pattern among MSA sites to feature as many or more small mammals and tortoises by NISP in relation to larger fauna (Thompson and Henshilwood, 2011).

Table 21: Composite Chi-squared values comparing the distribution of SMAs for each of the DK1 stratigraphic levels.

	MSA6	MSA7	MSA8	MSA9	MSA10	MSA11	MSA12	MSA13	MSA14	MSA15
LSA	**1526.93**	**1321.26**	**2440.44**	**759.05**	**212.53**	**187.40**	**229.54**	**287.77**	**2134.35**	**566.68**
MSA6		**3594.01**	**5910.80**	**2352.92**	**551.88**	**135.87**	**162.11**	**50.83**	**543.35**	7.94
MSA7			**146.76**	**105.75**	**784.44**	**1188.01**	**1367.47**	**972.55**	**4593.46**	**865.70**
MSA8				**489.54**	**1815.85**	**2692.96**	**2944.06**	**2389.53**	**7526.49**	**2255.59**
MSA9					**334.50**	**675.62**	**685.89**	**467.73**	**3175.19**	**413.55**
MSA10						**103.13**	**92.10**	**64.84**	**1238.01**	**118.25**
MSA11							**53.54**	**54.57**	**441.16**	**96.11**
MSA12								10.19	**410.47**	**43.96**
MSA13									**272.61**	**19.76**
MSA14										**78.16**
Bold values are significant at 0.01 level, un-bolded values are not significant.										

Where Cape dune mole-rats are somewhat less-abundant at DK1 (MSA layers 6, 11-15), hare and size 1 bovid counts increase. Composite Chi-squared values comparing the distribution of SMAs for each level are provided in Table 21; all but two comparisons are shown to be statistically different when each is examined head-to-head with another level, revealing a general pattern of variation in SMA composition between layers. In addition, Table 22 shows the Chi-squared values for each individual SMA in comparison to the previous level (Bonferroni correction has been applied). The scores are to be read in

comparison to the level to the right of the test statistic column. For example, the change in mole-rat abundance between layers MSA11 and MSA12 ($\chi^2 = 0.9$, $p = 0.331$) is not significant at the 0.05 level. The statistical results provided in Tables 2 and 3 and the %NISP of each taxon in Table 20 reveals that the SMAs differ significantly across nearly every level and that this relationship is driven mostly by fluctuating abundances of mole-rats, hares, and size 1 bovids across the MSA layers (Table 22). The differences between levels are far less affected by the changes in abundance of rock hyrax and small carnivores over time.

Table 22: Chi-squared values for the comparison of each individual SMA in relation to the abundance of the previous level.

	LSA	MSA6	MSA7	MSA8	MSA9	MSA10	MSA11	MSA12	MSA13	MSA14	MSA15
Mole-rats	**632.8**	**3591.4**	**142.0**	**478.1**	**303.2**	**49.3**	0.9	0.1	**248.0**	**73.7**	**-**
Hares	**896.7**	**1146.2**	**37.4**	**112.7**	**12.8**	5.3	**13.0**	**11.7**	**121.1**	**18.9**	**-**
Hyraxes	**225.7**	**95.9**	1.9	**86.0**	**20.2**	4.8	**26.0**	4.5	2.3	0.4	-
Carnivores	**113.2**	**24.6**	0.9	1.6	2.3	0.5	4.5	0.2	0.0	2.8	-
Size 1 bovid	**192.3**	**1582.2**	**100.3**	**270.1**	**277.4**	**96.7**	10.7	0.4	**11.7**	6.2	-
Bonferroni correction: significant at 0.05 level <0.01; bold values are significant.											

DK1- Taphonomic assessment of the small mammals

The DK1 specimens are very well preserved. In total, >70% of bone cortical surfaces are visible for analysis across all stratigraphic layers. Limiting factors such as bioerosion, bone surface exfoliation, matrix obfuscation, weathering, and rodent gnawing are minimally present in the assemblage, and complete specimens are relatively common (LSA = 18.7%, MSA6 = 13.9%, MSA7 = 13.0%, MSA8 = 13.1%, MSA9 = 12.9%, MSA10 = 13.4%, MSA11 =

16.2%, MSA12 = 14.1%, MSA13 = 13.7%, MSA14 = 11.4%, MSA15 = 10.2%) especially among Cape dune mole-rats, rock hyraxes, and small carnivores.

There is a significant positive correlation between stratigraphic level and ratio of complete to broken specimens ($r^2 = 0.365$, $p = 0.049$) where recent layers (i.e. LSA, MSA6, and MSA7) feature greater proportions of complete elements in comparison to older layers. Despite the fact that complete specimens increase in the more recent layers, there is a slight decrease in specimen length among those same levels. However, the relationship between specimen length and stratum age is not significant ($r^2 = 0.022$, $p = 0.680$). A Kruskal-Willis test for equality of medians demonstrates that there are significant differences in maximum fragment length of all specimens between stratigraphic layers ($H = 171.391$, $p < 0.001$) possibly as a result of differences in the number of complete specimens among the levels and/or the relative abundancies of small to larger taxa (i.e. mole-rats versus size 1 bovids and hares). The median lengths in mm for each level are: LSA=19, MSA6=15, MSA7=17, MSA8=16, MSA9=16, MSA10=15, MSA11=15, MSA12=17, MSA13=16, MSA14=18, MSA15=18.

The analysis of long bone fracture morphology can be employed as a gauge of pre- and post-depositional fragmentation (Villa and Mahieu, 1991). Typically, this type of analysis has been applied to large mammals, but Armstrong (2015) and Armstrong and Avery (2014) have demonstrated that it can also be used to assess small mammal fragmentation patterns. Like large

mammals, small mammal long bone shafts that were broken while ‘green’ tend to preserve more oblique fracture angles and V-shaped/curved fracture outlines whereas long bone shafts broken when ‘dry’ more often feature right fracture angles and transverse fracture outlines (Armstrong, 2015; Armstrong and Avery, 2014). After eliminating fractures that were the result of excavation damage, a total of 15,631 long bone fractures were analyzed. Table 23 reports fracture morphology frequencies and counts per taxonomic aggregate and stratum.

There is no correlation between the frequency of right fracture angles and superposition of stratigraphic layers for any of the small mammal taxonomic aggregates (mole-rat: r=0.006, *p*=0.820; size 1 bovid: r=0.018, *p*=0.693; hare: r=0.062, *p*=0.461; rock hyrax: r=0.004, *p*=0.852; carnivore: r=0.001, *p*=0.974). In other words, dry breaks do not significantly increase or decrease in abundance from the most recent to the oldest layers. To evaluate whether the DK1 bones were predominantly broken while ‘green’ or ‘dry,’ exact tests for goodness-of-fit were conducted comparing the observed distribution of fracture angle morphology frequencies (Table 23) for each small mammal taxonomic aggregate per layer in comparison to expected frequencies of oblique, right, and right/oblique fracture angles. The expected frequencies are assemblages of known breakage origin, the Fontbrégoua fresh bone breakage sample (fracture angle frequency of: oblique=65.5%, right=27.0%, oblique/right=7.5%) and the Sarrians dry bone breakage sample (fracture angle frequency of: oblique=8.2%,

right=65.4%, oblique/right=26.4%) reported by Villa and Mahieu, 1991. Breakage samples of <10 specimens were not included in goodness-of-fit tests.

All bone fracture angle distributions for each SMA per layer are statistically different (p=<0.05) in comparison to the Sarrians assemblage; none of the SMAs resemble dry bone breakage. A different pattern is apparent when comparing the Fontbrégoua assemblage where most of SMAs per layer reveal statistically indistinguishable distributions of fracture angles (32 of 38 comparisons of SMA with the Fontbrégoua assemblage); therefore, it is reasonable to conclude that most SMA long bones at DK1 were broken while fresh. However, there are six instances (mole-rats in MSA layers 7, 8, 12; hares in MSA14; hyraxes in MSA12, and size 1 bovids MSA6) where the fracture angle distributions are statistically different (p=<0.05) than the Fontbrégoua assemblage. This indicates that some post-depositional breakage occurred. Further, experimental studies have demonstrated that roughly 4.5% of long-bone breaks (among bovids) will be right fracture angles even when bone is broken while fresh (Marean et al, 2000a). All right fracture angle frequencies per taxonomic aggregate per layer at DK1 exceed 4.5%, so some of the bones were indeed broken when dry.

Table 23: Fracture angle and fracture outline frequencies for the DK1 long bones by small mammal taxonomic aggregate and stratum.

			Fracture angle (%)			Fracture outline			
Layer	Taxon agg.	n	Oblique (fresh)	Right (dry)	Oblique/ right	V-shaped (fresh)	Transverse (dry)	Intermediate	Transverse/curved
LSA	Mole-rat	824	74	24	2	79	17	1	3
	Bovid	628	74	25	1	82	16	1	1
	Hare	3	67	33	0	67	33	0	0
	Hyrax	28	75	25	0	71	24	2	3
	Carnivore	10	70	30	0	70	20	0	10
MSA6	Mole-rat	1318	69	28	3	73	22	1	4
	Bovid	2574	70	29	1	70	21	2	7
	Hare	711	74	24	2	81	15	1	3
	Hyrax	25	65	30	5	76	23	0	1
	Carnivore	8	100	0	0	100	0	0	0
MSA7	Mole-rat	1534	68	30	2	74	19	1	6
	Bovid	158	67	30	3	69	27	1	3
	Hare	39	82	17	1	78	20	0	2
	Hyrax	3	100	0	0	75	25	0	0
	Carnivore	3	100	0	0	100	0	0	0
MSA8	Mole-rat	2856	76	23	1	69	27	1	3
	Bovid	69	74	25	1	71	27	1	1
	Hare	13	90	10	0	85	15	0	0
	Hyrax	1	100	0	0	100	0	0	0
	Carnivore	1	0	100	0	0	100	0	0
MSA9	Mole-rat	1243	69	28	3	77	20	1	2
	Bovid	257	72	26	2	71	25	1	3
	Hare	74	74	25	1	60	34	1	5
	Hyrax	11	80	20	0	75	25	0	0
	Carnivore	1	100	0	0	100	0	0	0
MSA10	Mole-rat	467	75	24	1	68	27	2	3
	Bovid	486	69	30	1	76	15	3	6
	Hare	35	81	18	1	83	15	0	2
	Hyrax	8	100	0	0	72	28	0	0
	Carnivore	3	100	0	0	75	25	0	0
MSA11	Mole-rat	117	76	22	2	74	24	0	2
	Bovid	100	76	23	1	84	9	3	4
	Hare	7	70	30	0	70	30	0	0
	Hyrax	1	50	50	0	50	50	0	0
	Carnivore	0	-	-	-	-	-	100	-
MSA12	Mole-rat	148	80	18	2	78	19	1	2
	Bovid	318	68	31	1	69	28	1	2
	Hare	17	75	21	4	84	14	0	2
	Hyrax	11	100	0	0	86	14	0	0
	Carnivore	4	67	33	0	67	33	0	0
MSA13	Mole-rat	71	74	23	3	72	25	0	3
	Bovid	147	66	33	1	65	33	1	1
	Hare	24	72	25	3	80	15	2	3
	Hyrax	8	80	10	10	91	9	0	0
	Carnivore	1	100	0	0	50	0	0	50
MSA14	Mole-rat	141	68	31	1	74	23	1	2
	Bovid	715	70	28	2	73	21	2	4
	Hare	239	79	20	1	80	18	0	2
	Hyrax	35	69	30	1	82	17	1	0
	Carnivore	20	60	40	0	76	20	2	2
MSA15	Mole-rat	35	71	27	2	71	28	0	1
	Bovid	61	73	25	2	73	26	0	1
	Hare	13	85	15	0	78	19	0	3
	Hyrax	4	80	20	0	80	0	0	20
	Carnivore	0	-	-	-	-	-	100	-

Bone surface modification frequencies for each SMA by layer are reported in Table 24. Humans, mammalian carnivores, and raptors (both diurnal and nocturnal) are all potential accumulators of mammals at DK1; bone surface modifications that portents to the role of these predators have been included in this analysis. Experimental, actualistic, and ethnoarchaeological studies have demonstrated that humans (Henshilwood, 1997; Hockett, 1991; Lupo and Schmitt, 2005, Yellen, 1991ab), mammalian carnivores (Álvarez et al, 2012; Armstrong, 2015; Cochard, 2004; Lloveras et al 2008a; 2012; Rodríguez-Hidalgo et al, 2013; Schmitt and Juell, 1994), diurnal (Armstrong, 2015; Armstrong and Avery, 2014; Hockett, 1991; Lloveras et al, 2008b; 2014; Schmitt, 1995), and nocturnal (Armstrong, 2015; Lloveras et al, 2009a; Sanchis Serra, 2000) raptors accumulate and modify small mammal remains, and that different bone surface modification types and their relative frequencies can be used to differentiate between accumulators.

Table 24: Bone modification frequencies for each DK1 small mammal taxonomic aggregate. Taphonomic cluster designation based on the Euclidean cluster analysis (Fig. 27).

Layer	Taxon Agg.	Fragmentation	%Puncture	%Digestion	%Burning	%Cutmark	%Notch	%Pitting	Taphonomic Cluster
LSA	Mole-rats	1.35	0.2	3.4	11.2	1.8	0.0	1.1	Human
LSA	Size 1 bovids	1.69	0.5	1.1	8.1	5.1	2.9	0.8	Human
LSA	Hares	1.10	0.0	8.7	8.7	4.3	0.0	0.0	Human
LSA	Hyraxes	1.38	0.7	5.1	1.7	1.4	0.0	1.4	Human/Raptor
LSA	Carnivores	1.06	0.0	0.9	2.6	3.5	0.0	0.0	Human/Raptor
MSA6	Mole-rats	1.63	0.3	11.8	4.8	2.3	0.0	4.4	Human/Raptor
MSA6	Size 1 bovids	2.38	0.1	2.3	3.8	1.9	1.6	2.6	Human
MSA6	Hares	1.53	0.2	2.3	3.5	1.2	1.1	1.4	Human/Raptor
MSA6	Hyraxes	1.51	0.6	2.3	5.3	0.6	0.6	1.8	Human/Raptor
MSA6	Carnivores	1.40	0.0	18.8	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA7	Mole-rats	1.63	0.8	12.3	2.1	0.8	0.0	2.9	Human/Raptor
MSA7	Size 1 bovids	2.42	2.0	20.7	3.0	3.4	1.5	4.9	Human
MSA7	Hares	1.60	1.9	10.3	5.6	0.9	0.0	3.7	Human/Raptor
MSA7	Hyraxes	1.37	0.0	28.6	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA7	Carnivores	1.00	0.0	0.0	0.0	0.0	0.0	0.0	Diurnal raptor
MSA8	Mole-rats	1.83	0.5	7.2	1.4	0.3	0.0	1.4	Human/Raptor
MSA8	Size 1 bovids	1.50	0.0	6.7	0.0	0.0	3.3	5.0	Human/Raptor
MSA8	Hares	1.47	0.0	16.1	0.0	0.0	1.8	3.6	Human/Raptor
MSA8	Hyraxes	1.20	0.0	33.3	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA8	Carnivores	1.00	0.0	100.0	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA9	Mole-rats	1.81	0.6	16.7	1.3	0.2	0.0	2.2	Human/Raptor
MSA9	Size 1 bovids	1.76	1.4	20.7	2.3	0.9	2.7	4.5	Human/Raptor
MSA9	Hares	1.40	1.6	31.8	0.8	0.0	0.8	2.3	Nocturnal raptor
MSA9	Hyraxes	1.29	1.9	13.0	1.9	0.0	1.9	3.7	Human/Raptor
MSA9	Carnivores	1.00	33.3	0.0	0.0	0.0	0.0	0.0	Diurnal raptor
MSA10	Mole-rats	1.52	0.1	3.8	7.4	2.4	0.0	0.8	Human
MSA10	Size 1 bovids	1.50	1.1	6.6	5.1	6.0	3.9	1.9	Human
MSA10	Hares	1.56	0.0	3.2	2.1	1.1	2.1	0.0	Human/Raptor
MSA10	Hyraxes	1.39	0.0	5.3	1.8	0.0	1.8	0.0	Human/Raptor
MSA10	Carnivores	1.00	0.0	20.0	0.0	0.0	0.0	20.0	Diurnal raptor
MSA11	Mole-rats	1.74	0.8	17.4	0.8	1.1	0.0	2.2	Human/Raptor
MSA11	Size 1 bovids	2.17	4.3	22.3	0.0	3.3	1.9	5.2	Human/Raptor
MSA11	Hares	1.56	0.0	6.7	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA11	Hyraxes	1.40	0.0	14.3	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA12	Mole-rats	1.69	0.7	6.8	6.1	2.0	0.0	1.3	Human/Raptor
MSA12	Size 1 bovids	1.87	0.0	5.8	7.5	2.7	4.0	0.4	Human
MSA12	Hares	1.35	0.0	13.0	1.9	0.0	0.0	0.0	Human/Raptor
MSA12	Hyraxes	1.45	0.0	1.8	1.8	1.8	1.8	0.0	Human/Raptor
MSA12	Carnivores	1.44	0.0	37.5	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA13	Mole-rats	1.80	1.4	18.3	0.7	0.0	0.0	1.1	Nocturnal raptor
MSA13	Size 1 bovids	2.58	1.6	9.3	0.0	0.8	0.0	2.3	Nocturnal raptor
MSA13	Hares	1.56	0.0	18.0	0.0	0.0	0.0	2.0	Nocturnal raptor
MSA13	Hyraxes	1.58	0.0	5.3	0.0	0.0	0.0	0.0	Nocturnal raptor
MSA13	Carnivores	1.37	0.0	28.6	0.0	0.0	0.0	14.3	Diurnal raptor
MSA14	Mole-rats	1.72	0.7	12.2	7.0	3.5	0.0	2.4	Human
MSA14	Size 1 bovids	2.16	0.3	2.9	0.8	2.4	6.2	0.7	Human
MSA14	Hares	1.65	0.3	1.3	3.2	0.9	1.2	0.3	Human/Raptor
MSA14	Hyraxes	1.65	0.8	14.3	0.8	0.8	0.0	1.7	Human/Raptor
MSA14	Carnivores	1.35	0.0	8.6	0.0	2.9	0.0	2.9	Human/Raptor
MSA15	Mole-rats	1.58	0.0	33.9	0.9	0.0	0.0	1.8	Nocturnal raptor
MSA15	Size 1 bovids	2.36	0.0	11.9	0.0	0.0	0.0	3.4	Nocturnal raptor
MSA15	Hares	1.92	2.1	25.0	0.0	0.0	0.0	2.1	Nocturnal raptor
MSA15	Hyraxes	1.31	0.0	50.0	0.0	0.0	0.0	0.0	Nocturnal raptor

For example, mammalian carnivores and raptors digest the bones of small prey. However, diurnal raptors tend to consume fewer bones than nocturnal raptors and carnivores – diurnal raptors swallow ~25% of the bones of rabbit and guinea pig sized prey while nocturnal raptors and carnivores swallow ~65% and ~90%, respectively (Armstrong, 2015). Bones that are consumed by diurnal raptors tend to be axial skeletal elements, are often totally obliterated and deleted from an assemblage – diurnal raptors delete ~16% of rabbit and guinea pig sized prey skeletal elements while nocturnal raptors delete only ~8% of prey bones – and those that survive digestion exhibit 'extensive' digestion damage (Armstrong, 2015). Small mammal bones consumed by nocturnal raptors can be categorized as exhibiting 'moderate' digestion damage, include more appendicular elements, and are better preserved than those accumulated by diurnal raptors or carnivores (Armstrong, 2015). Carnivores thoroughly digest and masticate small mammal prey and often produce highly fragmented assemblages where their prey remains display 'extensive' digestion damage – the fragmentation ratio (NISP/MNE) of long-bones by carnivores is approximately 2.35 for rabbit- and guinea pig-sized prey while the ratio for diurnal and nocturnal raptors is only 1.44 and 1.70, respectively (Armstrong, 2015).

There are also differences in the frequencies of punctures and pits created by carnivore teeth and raptor beaks and/or talons. Diurnal raptors swallow fewer bones, consequently predation and feeding damage in the forms of punctures and pits are more often preserved in comparison to nocturnal raptors and

carnivores where the same marks are obscured by digestion damage and fragmentation (Armstrong, 2015; Armstrong and Avery, 2014). Signatures of human involvement in the accumulation of small mammals include cut-marked bone, percussion notches for marrow extraction (especially size 1 bovid long-bones and leporid hind limb bones), and burned bones (Fernández-Jalvo et al, 1999; Henshilwood, 1997; Hockett, 1991; Hockett and Haws, 2002; Hockett and Bicho, 2000; Parkington and Fischer, 2006; Tagliacozzo and Fiore, 1998; Tortosa et al, 2002; Yellen, 1991ab). Therefore the relative frequencies of digested, fragmented, pitted, punctured, cut marked, percussion notched, and burned bone are the suite of diagnostic bone surface modifications that are used to differentiate between human, carnivore, and raptor accumulation of small mammals.

Analysis of the taphonomic patterning and temporal variation for the SMAs at DK1 is presented in a principal components analysis (PCA) of bone modification proportions for all identifiable bone fragments (Fig. 26). The bone surface modifications considered in the PCA are those listed in the previous paragraph. Evidence of rodent gnawing was extremely rare and therefore excluded from the PCA as an accumulator diagnostic. Between 50-100% of bones recovered from modern porcupine dens exhibit gnawing (Brain, 1981; Lyman, 1994; Maguire et al, 1980; O'Regan et al, 2011); the lack of rodent-gnawed bone suggests that porcupines and other bone gnawing rodents played little – if any – role in the accumulation of bone at DK1.

In addition to the DK1 SMAs, a series of small mammal control assemblages that were accumulated by a known agent and feature comparable taphonomic analyses have been included in the PCA in order to assess similarities and differences between the DK1 assemblages and small mammal accumulations of known origin. These control assemblages include small mammals accumulated by (1) !Kung San foragers (Yellen, 1991ab; Armstrong, paper in preparation), (2) medium-sized carnivores (Armstrong, 2015; Lloveras et al, 2009a; Schmitt and Juell, 1994), (3) diurnal raptors (Armstrong, 2015; Armstrong and Avery, 2014), and (4) nocturnal raptors (Armstrong, 2015; Lloveras et al, 2009a).

Axis 1 of the DK1 PCA accounts for 37.7% of the variance while axis 2 accounts for 23.7%. Axis 1 discriminates between aggregates with human bone surface modifications (cut marks, burning, and percussion notches) versus modifications indicative of mammalian carnivore and raptor accumulation (digestion, fragmentation, tooth/beak/talon pits and punctures). Axis 2 discriminates between assemblages with differing frequencies of mammalian carnivore (fragmentation), nocturnal raptor (digestion), and diurnal raptor (pits and puncture) bone surface modifications. The SMAs with strong positive axis 1 scores exhibit greater frequencies of human-induced bone surface modifications while strong and moderate negative scores are indicative of predator-induced bone surface modifications. In regards to axis 2, strong positive scores represent aggregates with greater frequencies of carnivore modifications while intermediate

scores are associated with nocturnal raptors and strong negative scores associate with diurnal raptors.

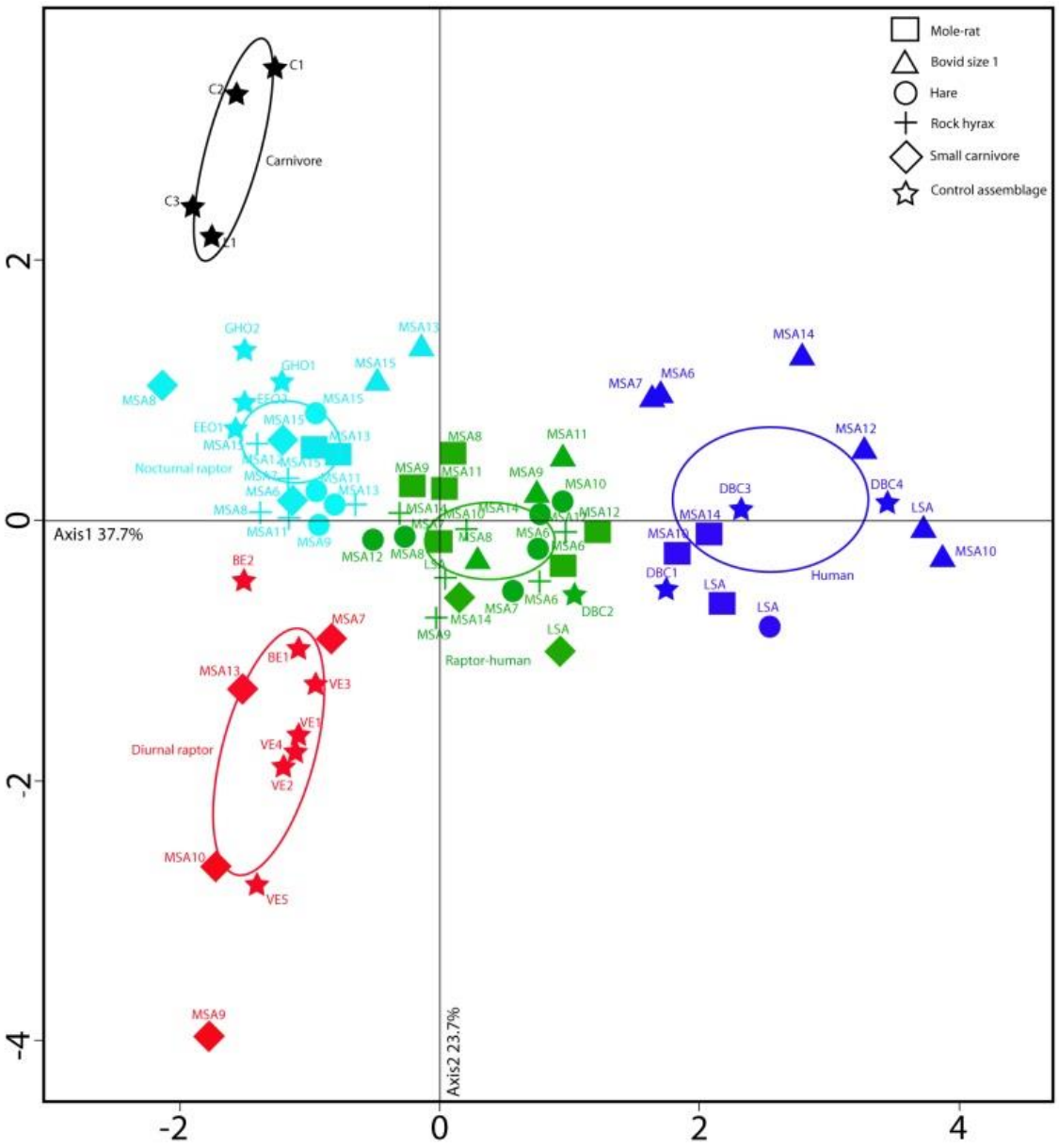


Figure 26: Principal components analysis of bone modification frequencies for the DK1 SMAs by stratum and control assemblages of known accumulation. Taphonomic aggregates are based on the cluster

analysis (Fig. 28): green=human/raptor, red=diurnal raptor-only, blue=human-only, black=carnivore-only, and light blue=nocturnal raptor-only. Barycentre ellipses represent the weighted relative center of each cluster. The control assemblages (predator followed by prey) are: BE1=bald eagle rabbit, BE2=bald eagle guinea pig, C1=coyote rabbit, C2= coyote guinea pig, C3=coyote rabbit, DBC1=human porcupine, DBC2=human hare, DBC3=human springhare, DBC4=human size 1 bovid, EEO1=European eagle owl rabbit, EEO2=European eagle owl rabbit, GHO1=great horned owl rabbit, GHO2=great horned owl guinea pig, L1=lynx rabbit, VE1=Verreaux's eagle mole-rat, VE2=Verreaux's eagle size 1 bovid, VE3=Verreaux's eagle hare, VE4=Verreaux's eagle hyrax, VE5=Verreaux's eagle small carnivore.

Figure 5 depicts the axis 1 scores which illustrate the variability between human and predator accumulated SMAs per stratum (positive scores denote human and negative scores denote predator accumulation). It is apparent that the rock hyrax and carnivore aggregates exhibit strong and intermediate negative scores across most layers, signifying little human involvement in their accumulation at DK1. Hares alternate between intermediate positive and negative scores suggesting anthropogenic accumulation in layers LSA, MSA6, MSA7, MSA10, MSA14, and non-anthropogenic accumulation in layers MSA8, MSA9, MSA11, MSA12, MSA13, MSA15. Cape dune mole-rats display strong positive scores in layers LSA, MSA6, MSA10, MSA12, MSA 14, intermediate negative scores in layers MSA7, MSA8, MSA9, MSA11, MSA13, and strong negative scores in layer MSA15. Size 1 bovids exhibit strong and intermediate positive scores in layers LSA, MSA6, MSA7, MSA8, MSA9, MSA10, MSA11, MSA12, MSA14, and intermediate negative scores in layers MSA13 and MSA15.

For Cape dune mole-rats, size 1 bovids, and hares, the taphonomic pattern of accumulation tends to alternate between strata where even numbered layers feature stronger anthropogenic input while odd layers favor greater predator contribution. This alternating pattern between layers with strong (even) and weak (odd) anthropogenic input was observed in the large mammal (Marean et al, 2000ab), micromorphology (Goldberg, 2000), and stone tool (Thackeray, 2000) accumulation analyses as well as Schweitzer's (1979; Tankard and Schweitzer, 1976) initial observations concerning site formation processes at DK1.

Based on the DK1 PCA analysis of bone surface modifications, it is clear that both humans and predators played roles in the accumulation of fauna and that their relative contributions varied by small mammal taxonomic aggregate per stratum. In order to assess which predator(s) contributed most heavily to the DK1 assemblage, a Euclidean hierarchical cluster analysis was conducted using the DK1 PCA axes 1 and 2 scores. This analysis includes the DK1 SMAs and the human, mammalian carnivore, diurnal and nocturnal raptor control assemblages. The expectation is that each SMA will cluster with the control assemblage(s) that it is most similar to taphonomically. The analysis was conducted with the CRAN-VEGAN algorithm for community paleoecology data (Oksanen et al, 2015) utilizing the R (version 2.15.3) statistical package.

Based on the cluster analysis, five taphonomic clusters are apparent (Fig. 6 and Table 24): mixed human and raptor (cluster 1), diurnal raptor-only (cluster 2), human-only (cluster 3), carnivore-only (cluster 4), and nocturnal raptor-only (cluster 5). In Figure 4, taphonomic clusters are defined by the cluster analysis results and are differentiated by color and barycentre ellipses are included representing the weighted relative center of each cluster.

The mixed human and raptor taphonomic cluster (1) contains the most SMAs and includes at least one aggregate from each stratigraphic level with the exceptions of layers MSA 13 and MSA 15 (each of which show heavy raptor input). The cluster can be characterized by moderate levels of fragmentation (1.56 NISP/MNE), burning (2.3%), cut marks (1.0%), percussion notches (0.2%), and beak/talon pits (2.3%), and low levels of beak/talon punctures (0.6%) and digestion (10.1%). There are only four SMAs associated with the diurnal raptor-only taphonomic cluster (2) all of which are small carnivores. These are characterized by high frequencies of punctures (4.6%) and pits (3.6%), low rates of fragmentation (1.18) and digestion (12.8%), and the absence of burned and cut marked bone, and percussion notches. There are 10 SMAs associated with the human-only cluster (3), nearly all of which are Cape dune mole-rat and size 1 bovid aggregates. This cluster is characterized by high degrees of burning (7.0%), cut marks (2.7%), and percussion notches (1.4%), moderate levels of fragmentation (1.77) and pits (1.5%), and low levels of punctures (0.3%) and digestions (3.7%). None of the DK1 SMAs group with the carnivore only cluster

(4). This group is defined by high levels of fragmentation (2.14) and digestion (90.0%), low levels of punctures (0.03%) and pits (0.02%), and the absence of burned and cut marked bone, and percussion notches. Fourteen SMAs – mostly from odd-numbered layers – make up the majority of the nocturnal raptor-only cluster (5). This cluster is characterized by moderate levels of fragmentation (1.58), punctures (1.0%), and digestion (61.6%), low levels of pitting (0.7%), and the absence of burned and cut marked bone, and percussion notches.

Figure 27: Variance in the DK1 PCA axis 1 scores showing predator and anthropogenic accumulations of the SMAs by stratum. Strongly positive scores denote human accumulation, moderate scores denote mixed predator accumulation, and strong negative scores denote non-human accumulation.

Based on the taphonomic analysis of bone surface modifications, the accumulation of small mammals at DK1 can be chiefly attributed to nocturnal raptors and humans. Mammalian carnivores appear to have had virtually no role in small mammal accumulation. The few SMAs that associate with diurnal raptors (Fig. 28) – all of which are small carnivores – feature small sample sizes, warranting some caution in regards to the attribution of their role in accumulations at DK1.

The roosting and feeding perch preferences of diurnal raptors provide another reason to be skeptical of their involvement at DK1. Diurnal raptors (such as eagles, hawks, and harriers) prefer nests and feeding perches in relatively open, elevated, and secure settings such as tree tops and steep cliffs (Hockey et al, 2005; Steyn, 1982). It would be highly unusual for a diurnal raptor to roost or perch within a cave, either inside on the cave wall or ground surface (Hockey et al, 2005; Steyn, 1982). They very well may have roosted or perched on the cliff face above DK1 and their prey remains may have accumulated below, near the cave opening. However, the archaeological deposits were excavated from near the back of the cave, upslope from the cave mouth where their prey remains

could not have accumulated. It is unlikely that massive quantities of discarded prey remains fell and moved upslope to the back of the cave. There is no taphonomic evidence to suggest that mammalian carnivores or rodents transported bones to the back of the cave after discard by diurnal raptors. Further, there is no evidence that humans accumulated the small carnivores at DK1, it is most likely that these prey were accumulated by nocturnal raptors as they exhibit digestion, punctures, and pits but the relatively small sample of compete bones distorts the identification of their accumulation.

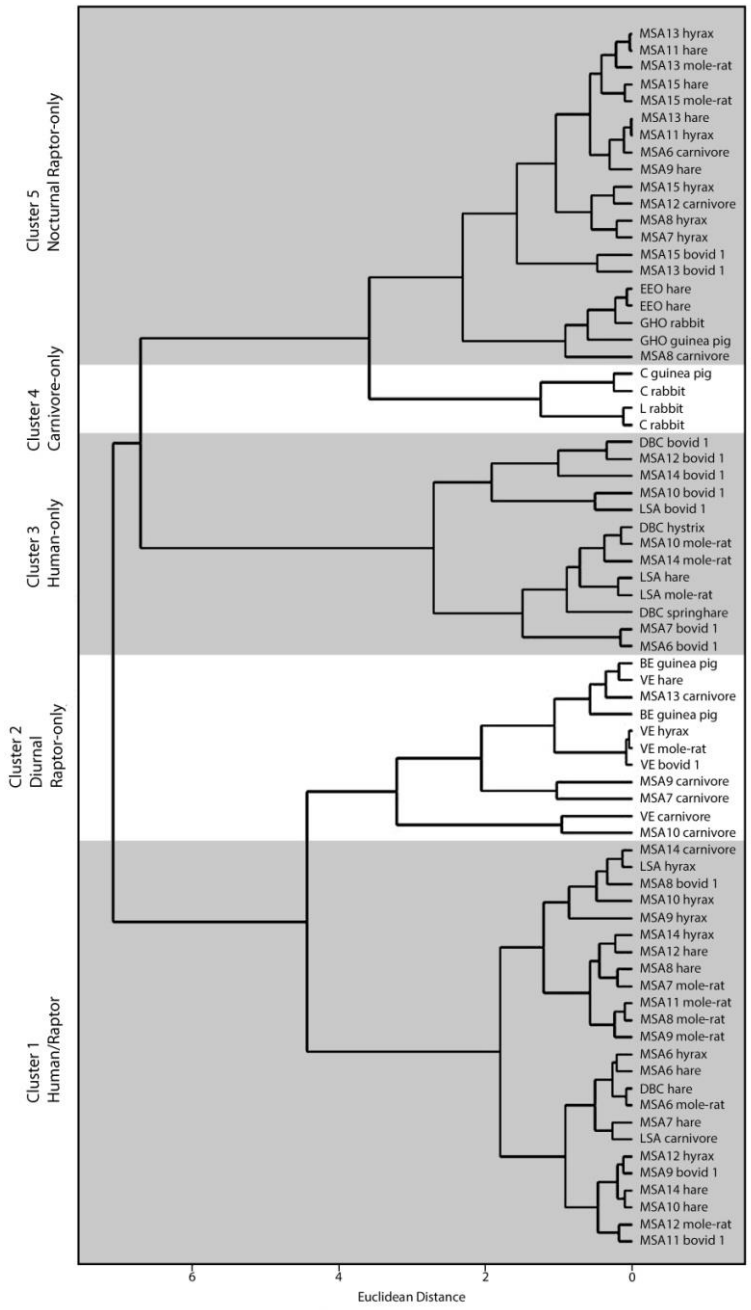


Figure 28: Euclidean cluster analysis of the DK1 PCA axes 1 and 2 scores for the SMAs by stratum. The control assemblages of known accumulation are included (predator followed by prey): VE=Verreaux's eagle, BE=bald eagle, GHO= great horned owl, EEO=European eagle owl, C=coyote, L=lynx, and DBC=Dobe Base Camps.

The present taphonomic analysis confirms Klein and Cruz-Uribe's (2000) hypothesis that nocturnal raptors played a role in small mammal accumulation at DK1. In some instances they appear to be the main accumulator (Fig. 28 and Table 24), while in others, their accumulations are mixed with human-accumulated small mammal remains (Fig. 28). Though it is impossible to unambiguously identify a specific nocturnal raptor taxon as the accumulator, Klein and Cruz-Uribe's (2000) identification of the Cape eagle owl is consistent with the prey taxa recovered at the site, the roosting and feeding preferences of the bird, and the general taphonomic pattern of the bones accumulated by raptors.

PP5-6 – Taxonomic composition

The PP5-6 specimen counts by stratum can be found in Table 25, which includes small mammals as well as all other identified fauna. As a species list and abundancies of small and large fauna have not been previously published for PP5-6, specimen counts and basic taxonomic identification by stratum of small and larger mammals, avifauna, tortoises, etc., have been included in order to illustrate the relative abundancies of different types of fauna at PP5-6. Large

Table 25: Taxonomic representation by NISP of each identified taxon and analytical aggregate by stratigraphic aggregate for the PP5-6 sample.

Taxon	Vernacular names	RBSR	BCSR	NWR	DBCS	OBS2	SGS	OBS1	SADBS	ALBS	LBSR	YBSR	YBS	Total
	Small mammals													
Bathyerugs suillus	Cape dune mole-rat	4	0	0	0	0	0	0	0	0	0	0	0	4
Genetta spp	Genet	0	0	1	0	0	0	0	0	0	0	0	0	1
Galerella pulverulenta	Cape grey mongoose	0	0	0	0	0	0	0	0	1	0	0	0	1
Lepus spp	Hare	1	0	0	1	0	0	0	4	2	0	0	0	8
Procavia capensis	Rock hyrax	0	0	0	0	1	0	0	1	1	1	0	0	4
	Indet small mammal	8	1	5	16	0	3	3	27	9	7	0	0	79
	Size 1 bovid	8	1	9	14	2	9	6	32	22	8	0	0	111
	Sum	21	2	15	31	3	12	9	64	35	16	0	0	208
	Other ID fauna													
	Amphibian	0	0	0	0	0	0	0	1	0	0	0	0	1
	Avian	0	0	0	0	0	0	0	0	5	0	0	0	5
	Size 2-4 bovid	98	311	296	1026	209	409	154	483	303	339	1	0	3629
	Indet large mammal	156	130	16	419	103	92	37	241	68	77	0	0	1339
	Micro mammal	2	0	0	1	5	0	1	0	1	0	0	0	10
	Seal	0	0	0	0	0	0	0	0	0	1	0	0	1
	Tortoise	47	24	95	161	47	44	13	33	6	55	0	0	525
	Ostrich Egg Shell	0	0	0	0	0	5	0	1	0	0	0	0	6
	Sum	303	465	407	1607	364	550	205	759	383	472	1	0	5516
	Total	324	467	422	1638	367	562	214	823	418	488	1	0	5724
	Analytical Aggregates													
	Small mammal group	13	1	6	17	1	3	3	32	13	8	0	0	97
	Size 1 bovid	8	1	9	14	2	9	6	32	22	8	0	0	111

mammals dominate the assemblage, only 4% of all mammals by NISP are small mammals. Size 1 bovids (53%) are the most abundant small mammal followed by small mammal bones for which the species is indeterminate (38%); these specimens consist mostly of rib and long bone shaft fragments. Other typical CFR small mammals (Cape dune mole-rat, hare, rock hyrax, and small carnivore) are represented in very low frequencies when calculated as either percentages of all mammals or as a fraction of only the small mammals.

In terms of small mammal relative abundance, PP5-6 differs from YST1, BBC, DKR, and DK1 in that they are not well represented. The ratio of small to large mammals is far more similar to PP13b in this regard; small mammals and size 1 bovids are 5% of all mammals at PP13b and 4% of mammals at PP5-6. A clear deviation from YFT1, BBC, DRS, and DK1 is the lack of Cape dune mole-rats at PP5-6. On average, mole-rats account for 55.3% of the fauna at these sites but constitute <2% of small mammals at PP5-6; there are no mole-rats reported from PP13b. Hares, rock hyraxes, and small carnivores comprise only 3.8%, 1.9%, and 1.0% of small mammals at PP5-6 respectively. Like PP13b, PP5-6 does not follow the “typical” pattern of MSA sites in the CFR in which many or more small mammals are present in relation to larger fauna.

In addition, there is a significant positive relationship between the small mammal NISP totals and the total number of mammal bones by stratigraphic

layer at PP5-6 (r = 0.59, p = 0.04). In other words, small mammal specimens do not cluster in any particular stratum, their abundance – or lack thereof – is simply associated with the total number of mammal bones recovered from each layer. Strata which yield relatively large numbers of mammal bone, such as layers DBCS and SADBS, are also the levels which feature the greatest numbers of small mammal remains. Conversely, strata that yield relatively few bones, such as layers OBS1 and OBS2, feature among the fewest small mammal remains.

PP5-6 – Taphonomic assessment of the small mammals

The PP5-6 specimens are not well preserved. In total, ~50% of bone cortical surfaces are visible for analysis across all layers, for comparison >70% of the DK1 bone cortical surfaces are preserved and visible. The PP5-6 specimens have been considerably affected by bone surface exfoliation and fragmentation. Bioerosion, matrix obfuscation, weathering, and rodent gnawing are each minimally present in the small mammal sample but none of these conditions (aside from matrix obfuscation) factor as prominently as exfoliation and fragmentation towards the lack of bone surface visibility. Complete specimens are not common among the PP5-6 sample as they account for only 6% of the assemblage by NISP compared to 14% at DK1. All of the complete specimens at PP5-6 are small compact bones (such as sesamoids, carpals, and tarsals), phalanges, or metapodials.

The average specimen length at PP5-6 is 12 mm whereas at DK1 the length is 17 mm. This difference is amplified by the fact that most of the DK1 specimens belong to the relatively small bodied Cape dune mole-rat whereas at PP5-6 most identified specimens are the comparatively larger size 1 bovids. The lack of original bone surfaces, dearth of complete specimens, and relatively small bone fragment size all demonstrate that the PP5-6 small mammal remains are not particularly well preserved. A consequence of this preservation state is that few bone features have been preserved. Twenty-six percent of mammal specimens are scrappy, cortical or trabecular bone fragments that lack diagnostic features and cannot be assigned to a specific skeletal element or taxon beyond bone fragment and mammal. The preservation state of PP5-6 renders both species and skeletal element attribution difficult and the tallying of MNIs and MNEs largely impracticable.

The assessment of long bone fracture morphology can only be conducted for size 1 bovids and indeterminate small mammal specimens as there are too few mole-rat, hare, rock hyrax, and carnivore long bone fragments needed in order to conduct meaningful analyses. In all, there are 145 size 1 bovid and indeterminate small mammal long bone fracture surfaces visible for analysis. The vast majority of these specimens can only be identified as long bone shaft fragments. Fracture morphology frequencies and counts per taxonomic aggregate and stratum can be found in Table 26. There is no correlation between the frequency of right fracture angles and age of stratigraphic level for

the size 1 bovids (r=0.068, *p*=0.862) or indeterminate small mammal (r=0.211, *p*=0.689) long bone fragments. In other words, dry breaks do not significantly increase or decrease in abundance from the most recent to the oldest layers.

Table 26: Fracture angle and fracture outline frequencies for the PP5-6 long bones by small mammal taxonomic aggregate and stratum.

				Fracture angle (%)			Fracture outline (%)		
Layer	Taxa	n	Oblique (fresh)	Right (dry)	Oblique/ righ	V-shaped (fresh)	Transverse (dry)	Intermediate	Transverse/curved
RBSR	Bovid size 1	8	1	0	0	63	25	13	0
	Indet. small mam.	4	25	0	75	0	25	0	75
NWR	Bovid size 1	13	54	23	23	69	23	0	8
	Indet. small mam.	6	33	67	0	50	33	0	17
DBCS	Bovid size 1	12	33	33	33	58	25	0	17
	Indet. small mam.	14	36	57	7	50	36	0	14
OBS2	Bovid size 1	1	1	0	0	1	0	0	0
	Indet. small mam.	0	-	-	-	-	-	-	-
SGS	Bovid size 1	7	86	14	0	86	14	0	0
	Indet. small mam.	0	-	-	-	-	-	-	-
OBS1	Bovid size 1	7	14	57	29	57	29	0	14
	Indet. small mam.	0	-	-	-	-	-	-	-
SADBS	Bovid size 1	22	55	14	32	55	9	5	32
	Indet. small mam.	14	50	36	14	57	21	0	21
ALBS	Bovid size 1	23	48	26	26	70	13	0	17
	Indet. small mam.	6	17	50	33	67	17	0	17
LBSR	Bovid size 1	2	0	0	1	0	50	0	50
	Indet. small mam.	6	17	33	50	50	17	0	33
Total	Bovid size 1	95	53	22	25	63	18	2	17
	Indet. small mam.	50	34	44	22	50	26	0	24

To evaluate whether the PP5-6 bones were predominantly broken while 'green' or 'dry,' exact tests for goodness-of-fit were conducted comparing the observed distributions of fracture angle morphologies (Table 26) for size 1 bovids and indeterminate small mammals for each layer in comparison to expected

frequencies of oblique, right, and right/oblique fracture angles based on the Fontbrégoua (fresh breakage sample) and the Sarrians (dry breakage sample) assemblages as described by Villa and Mahieu (1991).

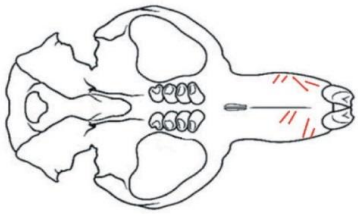
Fractured bone from only one-third of the sample aggregates by stratum have sufficient sample sizes (n ≥10) to compare to the Fontbrégoua and Sarrians assemblages. Of these, none of the size 1 bovid or indeterminate small mammal fracture angle frequency distributions are statistically different from the Fontbrégoua or Sarrians assemblages. These intermediate results indicate that numerous specimens were broken while fresh and that sufficient numbers of fragments retain indication of 'green' breakage, enough so that the frequencies of bone fractures are statistically indistinguishable from the Fontbrégoua assemblage. However, consequent portions of long bone fragments also exhibit 'dry' breakage, indicative of considerable post-depositional fragmentation. The result is that the samples are also statistically indistinguishable from the Sarrians assemblage where the vast majority of bones were broken when 'dry.' In sum, it appears that many size 1 bovid and indeterminate small mammal bones were broken while fresh, possibly by mammalian carnivores, humans, or predatory birds. The specimens were further fractured during the non-nutritive phase of the bones, perhaps as a result of trampling since a number of stratum exhibit evidence of intense human occupation and trampling (Karkanas et al, 2015).

Bone surface modification frequencies for each of the PP5-6 SMAs by stratum are reported in Table 27. Like DK1, and other MSA sites in southern Africa, humans, mammalian carnivores, diurnal and nocturnal raptors are all potential accumulators of fauna at PP5-6. Included in Table 27 is the suite of bone surface modifications indicative of the predator(s) responsible for small mammal accumulation at PP5-6.

Table 27: Bone modification frequencies for the PP5-6 small mammal taxonomic aggregate. Taphonomic cluster designation based on the Euclidian cluster analysis (Fig.31).

Layer	Taxon Agg.	Fragmentation	%Puncture	%Digestion	%Burning	%Cutmark	%Notch	%Pitting	Taphonomic Cluster
RBSR	Small mam. group	1.44	4.6	15.4	0.0	0.0	0.0	3.7	Mixed raptor
	Size 1 bovid	1.33	0.0	0.0	0.0	0.0	0.0	0.0	Mixed raptor
NWR	Small mam. group	2.00	11.0	0.0	0.0	0.0	0.0	5.0	Mixed raptor
	Size 1 bovid	1.80	0.0	0.0	33.3	0.0	0.0	0.0	Human
DBCS	Small mam. group	2.40	5.9	0.0	2.9	0.0	0.0	0.0	Nocturnal raptor
	Size 1 bovid	1.56	0.0	0.0	0.0	0.0	0.0	1.0	Mixed raptor
OBS2	Size 1 bovid	1.00	0.0	0.0	5.0	0.0	0.0	0.0	Mixed raptor
SGS	Small mam. group	1.50	0.0	33.3	0.0	0.0	0.0	0.0	Nocturnal raptor
	Size 1 bovid	1.50	0.0	0.0	0.0	0.0	0.0	1.0	Mixed raptor
OBS1	Small mam. group	1.50	0.0	0.0	11.1	0.0	0.0	0.0	Mixed raptor
	Size 1 bovid	1.50	0.0	0.0	16.7	0.0	0.0	0.0	Mixed raptor
SADBS	Small mam. group	2.46	0.0	3.1	6.3	0.0	0.0	0.0	Nocturnal raptor
	Size 1 bovid	1.68	1.5	3.1	6.3	0.0	0.0	2.1	Mixed raptor
ALBS	Small mam. group	1.86	0.0	0.0	0.0	0.0	0.0	0.0	Nocturnal raptor
	Size 1 bovid	1.57	3.2	0.0	13.6	0.0	0.0	1.3	Mixed raptor
LBSR	Small mam. group	1.67	1.3	1.0	4.3	5.3	0.0	0.0	Human
	Size 1 bovid	1.14	0.0	0.0	0.0	0.0	0.0	0.0	Mixed raptor

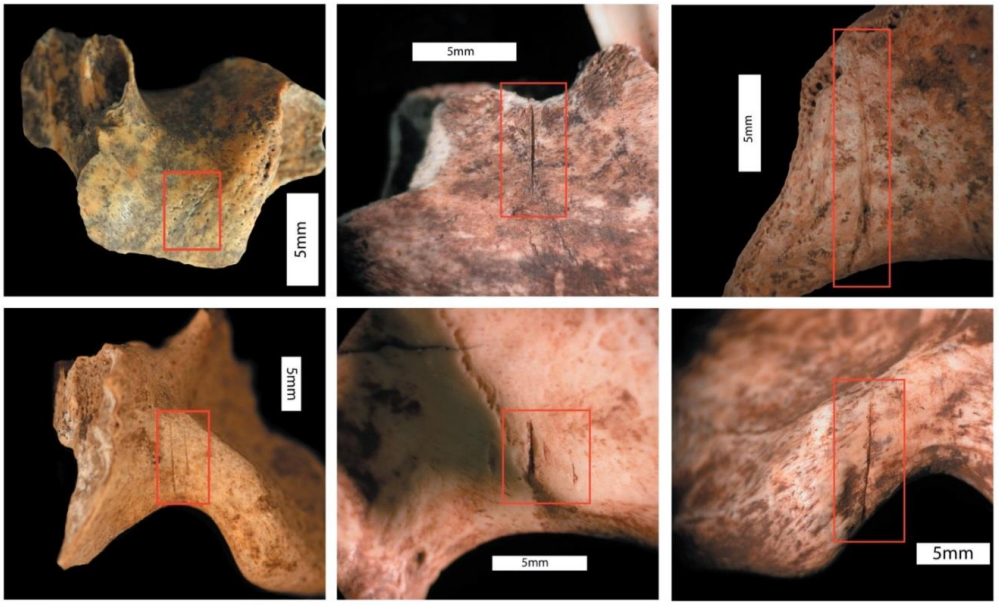
Premaxilla

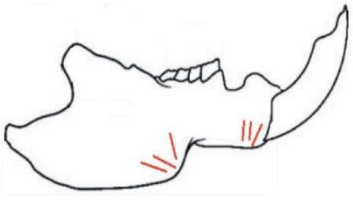


Premaxilla

Layer	LSA	MSA6	MSA7	MSA8	MSA9	MSA10	MSA11	MSA12	MSA13	MSA14	MSA15
%Cutmark	9.8	16.3	15.9	9.7	14.3	13.5	0.0	22.2	0.0	18.8	0.0

Mandible

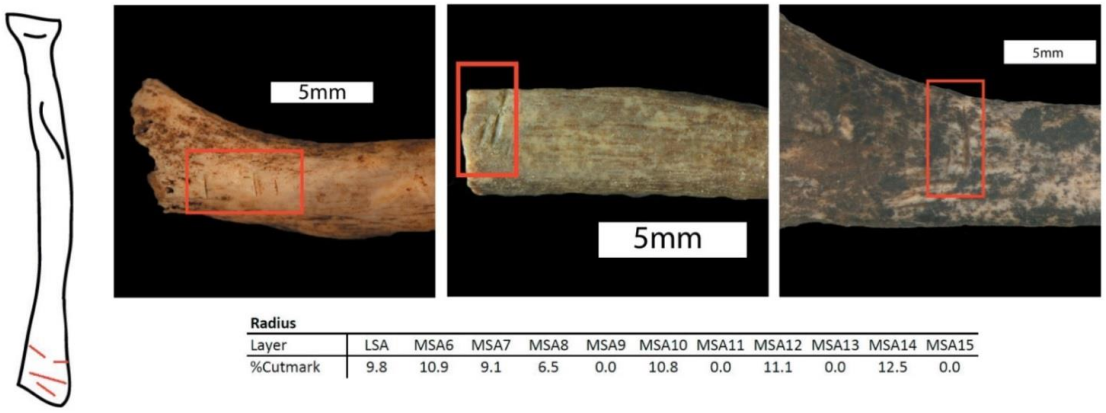




Mandible: Anterior*, Coronoid#

Layer	LSA	MSA6	MSA7	MSA8	MSA9	MSA10	MSA11	MSA12	MSA13	MSA14	MSA15
%Cutmark*	23.5	13.0	22.7	12.9	0.0	24.3	0.0	0.0	0.0	6.3	0.0
%Cutmark#	13.7	12.0	9.1	19.4	14.3	10.8	50.0	22.2	0.0	12.5	0.0

Radius



Radius

Layer	LSA	MSA6	MSA7	MSA8	MSA9	MSA10	MSA11	MSA12	MSA13	MSA14	MSA15
%Cutmark	9.8	10.9	9.1	6.5	0.0	10.8	0.0	11.1	0.0	12.5	0.0

Ulna

Ulna

Layer	LSA	MSA6	MSA7	MSA8	MSA9	MSA10	MSA11	MSA12	MSA13	MSA14	MSA15
%Cutmark	3.9	6.5	0.0	3.2	0.0	5.4	0.0	11.1	0.0	6.3	0.0

Tibia

Tibia

Layer	LSA	MSA6	MSA7	MSA8	MSA9	MSA10	MSA11	MSA12	MSA13	MSA14	MSA15
%Cutmark	15.7	25.0	27.3	16.1	42.9	21.6	0.0	33.3	0.0	31.3	0.0

Figure 29: Photographs showing cut marks to the premaxilla and mandible (anterior portion and coronoid process) as well as the distal radius, ulna, and tibia of Cape dune mole-rats from MSA layers at DK1. Line drawings show the locations of recurrent cut marks indicative of skinning for these skeletal elements. The tables report the frequencies of cut marks at the specific skeletal elements by stratum.

An analysis of the taphonomic patterning and temporal variation of the SMAs at PP5-6 is provided in a PCA of the bone modification proportions for all identifiable bone fragments (Fig. 30). The bone surface modifications considered in the PCA are those presented in Table 27. Also included in the PCA are the small mammal assemblages of known accumulation discussed previously: (1) !Kung San foragers, (2) medium-sized carnivores, (3) diurnal raptors, and (4) nocturnal raptors. Like DK1, the lack of rodent- gnawed bone (only one specimen exhibits gnaw marks) indicates that porcupines and other rodents played little role in the accumulation of bone at PP5-6; therefore, rodent gnawing has been excluded from the PCA as an accumulator diagnostic.

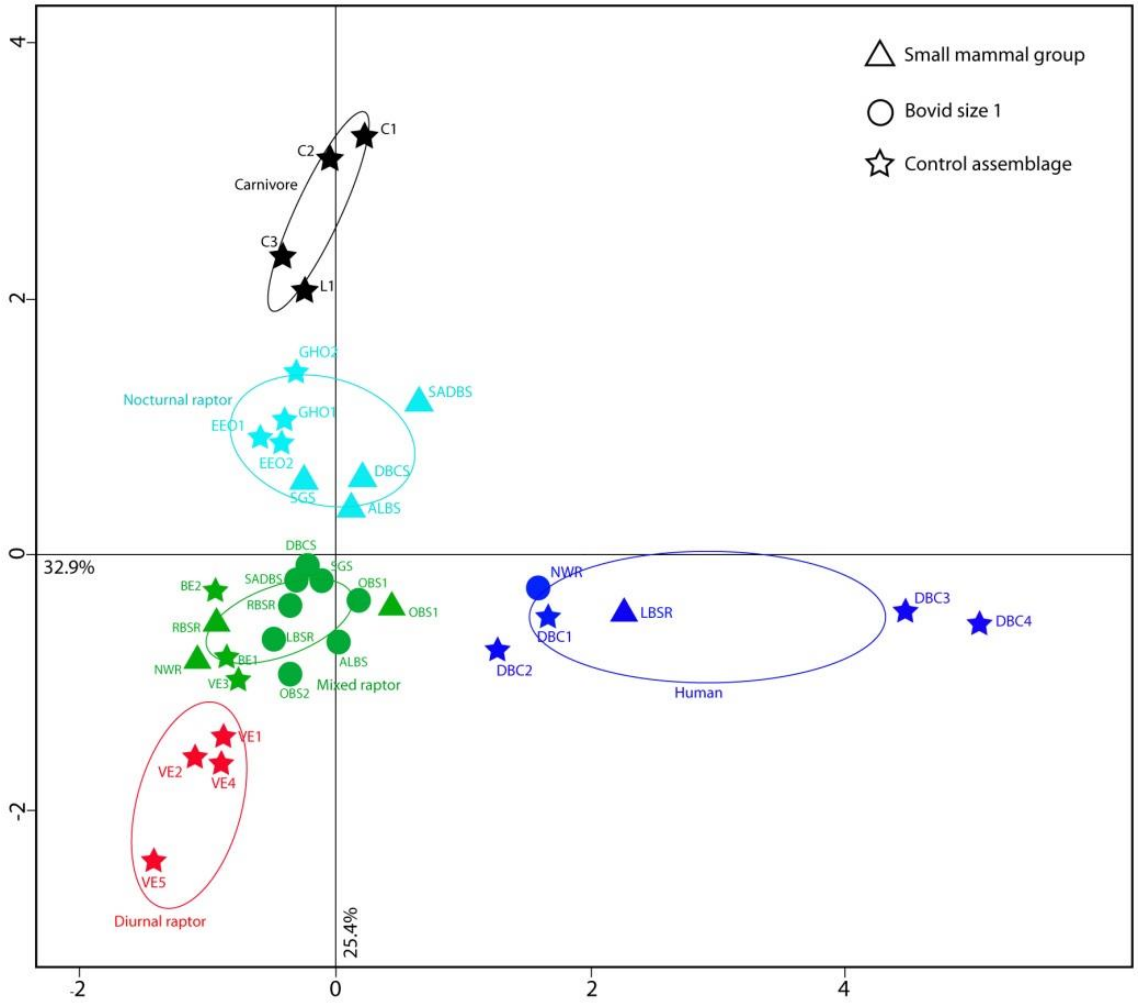


Figure 30: Principal components analysis of bone modification frequencies for the PP5-6 SMAs by stratum and control assemblages of known accumulation. Taphonomic aggregates are based on the cluster analysis (Fig. 32): green = mixed diurnal and nocturnal raptor, red = diurnal raptor-only, blue = human-only, black = carnivore-only, and light blue = nocturnal raptor-only. Barycentre ellipses represent the weighted relative center of each cluster. The control assemblages (predator followed by prey) are: BE1=bald eagle rabbit, BE2=bald eagle guinea pig, C1=coyote rabbit, C2= coyote guinea pig, C3=coyote rabbit, DBC1=human porcupine, DBC2=human hare, DBC3=human springhare, DBC4=human size 1 bovid, EEO1=European eagle owl rabbit, EEO2=European eagle owl rabbit, GHO1=great horned owl rabbit, GHO2=great horned owl guinea pig, L1=lynx rabbit, VE1=Verreaux's eagle mole-rat, VE2=Verreaux's eagle size 1 bovid, VE3=Verreaux's eagle hare, VE4=Verreaux's eagle hyrax, VE5=Verreaux's eagle small carnivore.

The PP5-6 PCA axis 1 accounts for 32.9% of the variance while axis 2 accounts for 25.4%. The axis 1 vector discriminates between aggregates with human bone surface modifications (cut marks, burning, and percussion damage) and modifications indicative of mammalian carnivore and raptor accumulation (digestion, tooth/beak/talon pits, and punctures, but excluding fragmentation as the vector is moderately positive along axis 1 in this PCA). Axis 2 discriminates between assemblages with differing frequencies of carnivore (fragmentation), nocturnal raptor (digestion), and diurnal raptor (pits and puncture) bone surface modifications. The SMAs with strongly positive axis 1 scores exhibit greater frequencies of human-induced bone surface modifications while moderately positive and negative scores are indicative of predator-induced bone surface modifications. Strongly positive scores along axis 2 represent aggregates with greater frequencies of carnivore modifications whereas moderately positive scores reveal association with nocturnal raptors. Negative scores along axis 2 are associated with diurnal raptors.

Figure 31 depicts the axis 1 scores which illustrates the irregularity of human-accumulated SMAs over time in comparison to predator-accumulated bone (strong positive scores denote human, while moderate and negative scores denote predator accumulations). Only the NWR size 1 bovids and LBSR small mammal group have strongly positive scores, signifying human accumulation of these aggregates. These two human accumulated aggregates are temporally separate, dating to 61(±4) ky and 81(±4) ky, respectively. All other size 1 bovid

and small mammal groups have strong negative or moderate axis 1 scores suggesting non-human accumulation for the bulk of the small mammal faunas at PP5-6.

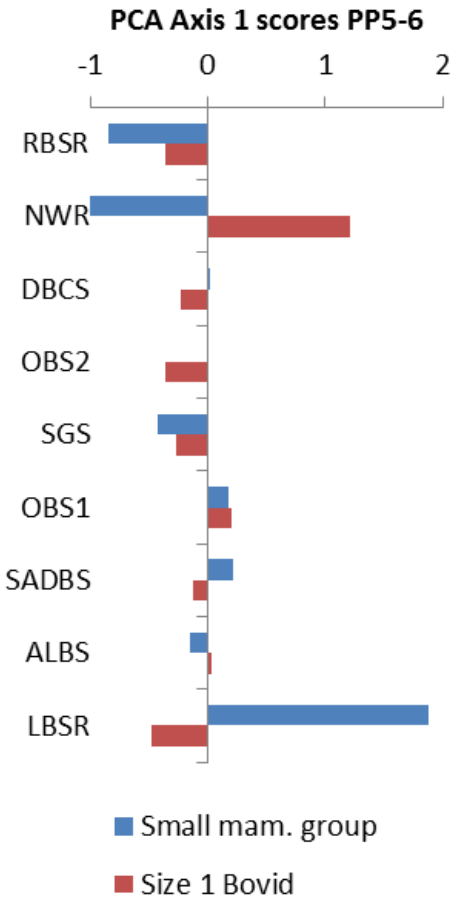


Figure 31: Variance in the PP5-6 PCA axis 1 scores showing predator and anthropogenic accumulations of the SMAs by stratum. Strongly positive scores denote human accumulation, moderate scores dente mixed predator accumulation, and strong negative scores denote non-human accumulation.

The taphonomy of PP5-6 indicates that predators were largely responsible for the accumulation of small fauna. In order to assess which non-human predator(s) contributed most heavily to the PP5-6 assemblage, a Euclidean hierarchical cluster analysis was conducted using the axes 1 and 2 scores of the PP5-6 PCA. This analysis includes the PP5-6 SMAs as well as the human, mammalian carnivore, diurnal and nocturnal raptor control assemblages. The expectation is that each SMA will cluster with the control assemblage(s) that it most closely resembles.

Based on the cluster analysis (Fig. 32), five taphonomic clusters are apparent (Fig. 32 and Table 27): diurnal raptor-only (cluster 1), nocturnal raptor-only (cluster 2), mixed diurnal and nocturnal raptor (cluster 3), carnivore-only (cluster 4), and human-only (cluster 5). In Fig. 30, taphonomic clusters are differentiated by color and barycentre ellipses are included representing the weighted relative center of each cluster.

The human-only taphonomic cluster (5) includes NWR size 1 bovids, LBSR small mammal group, and the human accumulated control samples. The factors driving the association of the two archaeological samples with the human-accumulated control assemblages are similar levels of fragmentation (1.7 NISP/MNE), the presence of burned (9.3%) and cut-marked bone (3.9%), and minimal frequencies of digested bone (0.01%), punctures (0.01%), and pits (0.01%). There are no PP5-6 SMAs associated with the diurnal raptor-only (1)

taphonomic cluster; it consists of four of the five prey aggregates accumulated by Verreaux's eagle. There are four PP5-6 SMAs associated with the nocturnal raptor-only cluster (2), which can be attributed to the small mammal group aggregate. This cluster is characterized by elevated levels of fragmentation (1.80), the presence of digested bone (37.6%), punctured (1.0%) or pitted bone (1.5%), the lack of cut marks and percussion notches, and low frequencies of burned bone (0.9%). None of the PP5-6 SMAs group with the carnivore-only cluster (4). This group is defined by high levels of fragmentation (2.14) and digestion (90.0%), low levels of punctures (0.03%) and pits (0.02%), and the absence of burned, cut-marked, and percussion-notched bone.

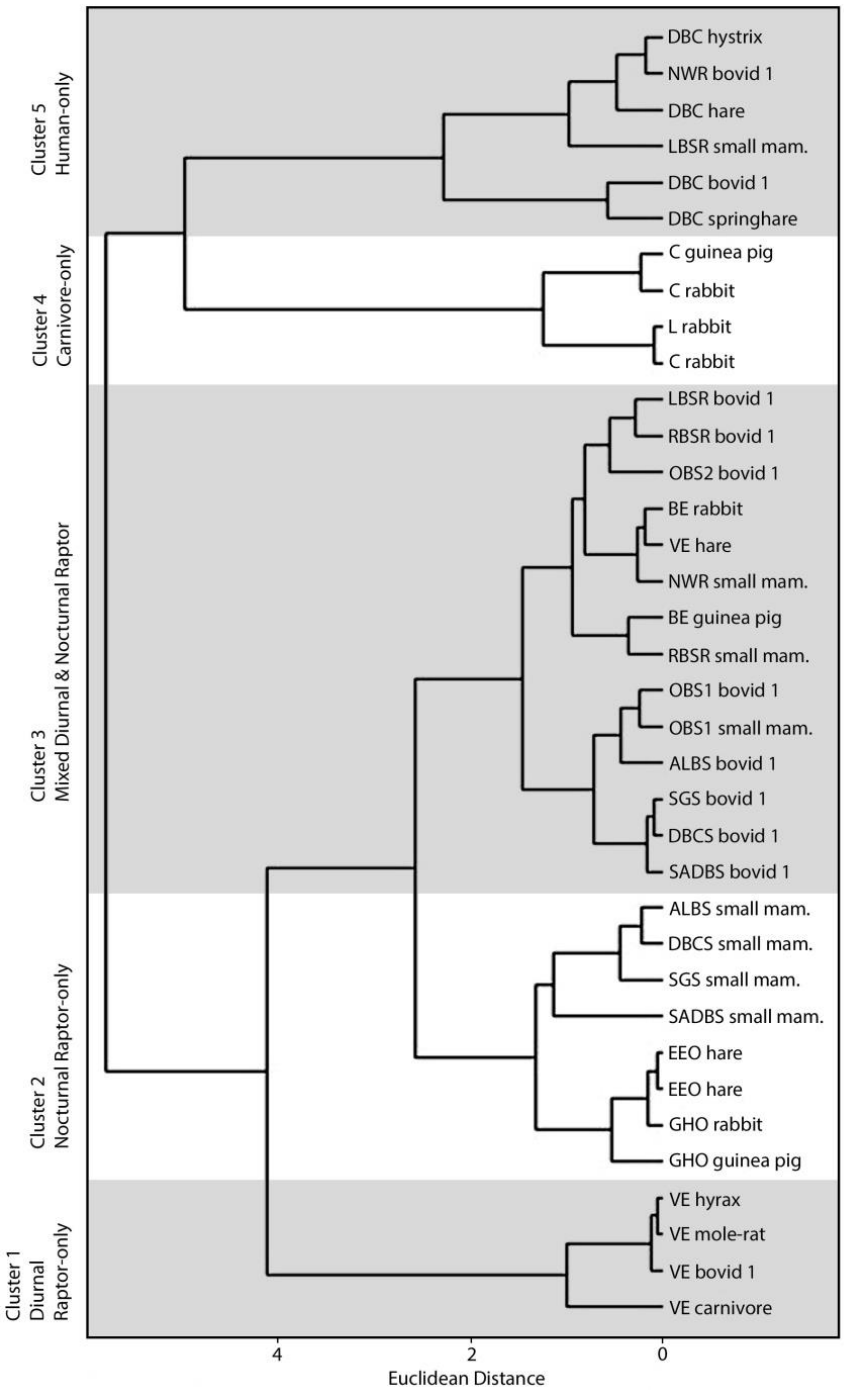


Figure 32: Euclidean cluster analysis of the PP5-6 PCA axes 1 and 2 scores for the SMAs by stratum. The control assemblages of known accumulation are included (predator followed by prey): VE=Verreaux's eagle, BE=bald eagle, GHO= great horned owl, EEO=European eagle owl, C=coyote, L=lynx, and DBC=Dobe Base Camps.

The mixed raptor cluster (3) is comprised of 11 PP5-6 SMAs as well as one Verreaux's eagle and two bald eagle control sample assemblages. In addition to clustering with these three diurnal raptor prey aggregates, this cluster shares some taphonomic affinities with nocturnal raptors in the forms of digested bone and fragmentation, and to a lesser extent, the human-accumulated assemblages in relation to the presence of burned bone. This is apparent in Fig. 30 where the mixed raptor cluster is situated near the diurnal and nocturnal raptor-only clusters, supporting the hypothesis that both diurnal and nocturnal raptors contributed to the accumulations. A few of the mixed cluster aggregates fall near the human-only cluster due to the shared presence of burned bone. However, the relative frequencies of other taphonomic indicators and the presence of burned bone suggest greater affinities with the raptor assemblages as opposed to human accumulation. The mixed cluster (3) is characterized by moderate levels of fragmentation (1.47) and punctures (1.3%), some digestion (3.7%) and burning (4.1%), and the absence of cut marks, and percussion notches.

Based on the similarities of bone surface modifications, the accumulation of small mammals at PP5-6 can largely be attributed to nocturnal and diurnal raptors. Humans played a minimal role in the accumulation of the fauna but were likely the primary agent responsible for the accumulation of two SMAs in two separate strata. Yet the presence of burned bone in layers SADBS and OBS1 suggests that humans may have played some role in accumulation of specimens

in these strata. However, the bones from these layers also retain evidence of raptor contribution and this evidence is greater in relative abundance than the evidence for human accumulation. It is also possible that the bones were deposited by raptors and subsequently incorporated into sediments that were successively burned. Mammalian carnivores seem to have had no role in small mammal accumulation at PP5-6.

The role of diurnal and nocturnal raptors in the accumulation of the PP5-6 sample is supported by the types and frequencies of observed bone surface modifications. In addition, the topographical features in the immediate vicinity of the PP5-6 rockshelter are agreeable to raptor roost preferences. The steep and inaccessible quartzitic cliffs above the site provide ideal nest localities for diurnal raptors while the rockshelter below provides a catchment for prey remains dropped from nests and feeding perches above. Today, jackal buzzards (*Buteo rufofuscus*) roost on the cliffs near the rockshelter and Verreaux's eagles (*Aquila verreauxii*) have been seen perched on cliffs near the site, once while gripping a kill (author personal observation). In contrast to DK1, it is reasonable to suppose that small prey remains collected by diurnal raptors made their way into the PP5-6 faunal assemblage. As for nocturnal raptors, there are active nests inside some of the caves and rockshelters in the immediate vicinity of PP5-6. Barn owls (*Tyto alba*) and spotted eagle-owls (*Bubo africanus*) have been observed in the area by the author and collections of owl pellets have been noticed in the caves and rockshelters adjacent to PP5-6 (E. Fisher, personal communication).

As with the diurnal raptor prey remains, it is reasonable to imagine that owl pellets and prey bones were discarded on the rockshelter floor or expelled from nests and found their way into the PP5-6 faunal sample.

DISCUSSION

Human accumulation of Cape dune mole-rats at DK1

Cape dune mole-rat accumulations are common at Later and Middle Stone Age sites in the CFR and the question of their accumulation origins has been a persistent question. Researchers have argued that some LSA accumulations of mole-rats were human derived (particularly those that are <5,000 year old) while MSA accumulations were most likely collected by non-human predators. For instance, researchers contend that the mole-rats from LSA sites or strata at Pancho's Kitchen Midden (Jerardino, 1998), Eland's Bay Cave (Klein and Cruz-Uribe, 1987), DK1 (Avery et al, 1997; Klein and Cruz-Uribe, 2000; Schweitzer, 1979), BBC (Henshilwood, 1997), Byneskranskop 1 (Schweitzer and Wilson, 1982), and Tortoise Cave (Klein and Cruz-Uribe, 1987; Robey, 1987) are probably human accumulated. In some cases, the evidence for human agency centers on the presence of cut and burned bone (LSA portions of DK1 and BBC). In other instances, more tentative forms of evidence, such as the co-occurrence of mole-rat bones in strata which also contain anthropogenic materials (Byneskranskop 1, Eland's Bay Cave, and Tortoise Cave), or the lack

of suitable raptor roosting space near the mole-rat accumulations, or both factors (Pancho's Kitchen Midden and Eland's Bay Open), have been evoked as evidence for human agency.

These latter arguments are challengeable as they suppose that only raptors or humans could be responsible for mole-rat accumulation and discount carnivores and other means of bone accumulation; taphonomic analyses which could clarify this have not been reported for these LSA sites. With the exception of Henshilwood's (1997) ethnoarchaeological documentation and comparison of mole-rat bones burned by contemporary people and LSA humans at BBC, none of the studies explicitly report and describe the counts and anatomical patterning of bone surface modifications, factors that could be used to illuminate the origin of mole-rat bone accumulation. Nevertheless, it has been largely accepted that humans were frequently responsible for mole-rat accumulations during the LSA.

Conversely, MSA accumulations of Cape dune mole-rats at DK1 (Avery et al, 1997; Klein and Cruz-Uribe, 2000; Marean et al, 2000b), BBC (Henshilwood, 1997; Badenhorst et al, 2014), and YFT1 (Avery et al, 2008; Halkett et al, 2003; Klein et al, 2004) as well as LSA layers >5,000 years old at Elands Bay Cave, Tortoise Cave, and Byneskranskop 1 are generally thought to be non-human accumulated. The reported presence of digested bone similar in appearance to bone generated by owl gastric etching (MSA portion of DK1 and layers >5,000 years old at Elands Bay Cave and Byneskranskop 1) and the lack of cut-marked

and burned bone (MSA portion of BBC) have led researchers to suggest that MSA accumulations of mole-rats are likely not the result of human activities. Ancillary evidence in support of this interpretation, such as the presence of bone accumulators like porcupine and small carnivores in layers that also contain mole-rats (YFT1), the disproportionately high frequencies of juvenile size 1 bovids (particularly *Raphicerus spp.*) and the suitability of these locales as raptor roosts (MSA portion of DK1 and layers >5,000 years old at Tortoise Cave), have also been cited as evidence for non-human accumulation of mole-rats. While various taphonomic factors have been evoked as evidence for raptor and/or carnivore accumulation of mole-rats at MSA sites and LSA sites >5,000 years old, analyses that plainly describe bone surface modifications, anatomical patterning, and the overall frequency of modifications (or the lack thereof) in these assemblages have not been reported.

The bone surface modification patterns found on mole-rats at DK1 are unique, the LSA and MSA assemblages exhibit clear evidence of human agency and this paper represents the first comprehensive taphonomic evidence for the human accumulation of Cape dune mole-rats during the MSA. The primary forms of evidence are cut-marked and burned bone (much of which is calcined), frequencies of which are reported in Table 24. In the LSA and MSA portions of the DK1 assemblage, 81% of cut marks occur in these anatomical locations (Fig. 29): the underside of the premaxilla (14%), the anterior portion (16%) and coronoid process of the mandible (13%), the distal ulna (4%), distal radius (10%),

and the distal tibia (23%). The remaining cut marks fall among the other skeletal elements (such as the innominate, humerus, femur, calcaneus, incisors, and vertebrae) in less frequent and more random patterns (19%). Included in Fig. 29 are summarizes of cut mark frequencies on mole-rat bones by skeletal element for each stratum at DK1.

The anatomical location of cut marks on Cape dune mole-rat bones at DK1 are analogous to patterns of damage frequently associated with the skinning of small, fur-bearing mammals (Charles, 1997; Charles et al, 1994; Fairnell, 2008; Lloveras et al, 2009b; Mallye, 2011; Rowley-Conwy, 1994; Strid, 2000; Trolle-Lassen, 1987; Vigne and Guilaine, 2004). Cut marks are the most recognizable indication of skinning left on the bones of a carcass and the documentation of cut marks to the bones of small, fur-bearing mammals such as canids (Charles, 1997; Compagnoni et al, 1997; Fairnell and Barrett, 2007; Martín et al, 2014; Strid, 2000; Vigne and Guilaine, 2004; Wigh, 1997; Yeshurun et al, 2009), erinaceids (Fernández-Jalvo et al, 1999), felids (Charles, 1997; Crezzini et al, 2014; Strid, 2000; Vigne and Guilaine, 2004; Yravedra, 2005), herpestids (Parkington and Fisher, 2006), lagomorphs (Charles, 1997; Charles et al, 1994; Lloveras et al, 2009b), mustelids (Charles, 1997; Fairnell and Barrett, 2007; Mallye, 2011; O'Connor, 1991; Parks, 2003; Parkington and Fisher, 2006; Richter, 2005; Strid, 2000; Trolle-Lassen, 1986; 1987; Zeiler, 1987; Wigh, 1997), and rodents (Charles, 1997; Tamplin et al, 1983; Trolle-Lassen, 1987; Zeiler, 1987; Wigh, 1997) present a consistent and robust anatomical pattern of cut

marks for the indication of skinning. The pattern of cut marks left on specific mole-rat skeletal elements at DK1 are interpreted as such evidence.

This pattern consists of the clustering of cut marks at the (1) the maxilla and premaxilla as well as the eye orbits of the cranium, (2) the corpus and ascending ramus of the mandible, (3) the lower limbs (particularly the distal radius, ulna, and tibia), and occasionally (4) podial elements (such as the calcaneus, metapodials, and phalanges) which varies by species and seems to depend on whether fur is present on the feet, if that fur is desirable, and if attached claws are preferred. Mole-rat feet are hairless (and small) which may account for there being fewer identified cut marks on podial elements. The mole-rat skeletal elements that consistently exhibit cut marks (mandibles, crania, and distal limb elements) at DK1 are consistent with the pattern of skinning damage documented in numerous studies and include a range of small, fur-bearing mammals.

In some instances, patterns of discarded skeletal elements – particularly the relative overabundances of podial bones and mandibles in relation to limb and axial skeletal elements – associated with small mammal field processing has been identified as evidence for skinning and fur utilization, especially in regards to canids and felids (Baxter and Hamilton-Dyer, 2003; Charles, 1997; Compagnoni et al, 1997; Klein, 1973; Schmidt, 1999; Tamplin et al, 1983). However, this skeletal-part pattern is not always associated with the processing

of fur-bearing mammals for their skins (Charles et al, 1994; Crezzini et al, 2014; Fairnell and Barrett, 2007; Martín et al, 2014; Parkington and Fisher, 2006; Wigh, 1997; Yeshurun et al, 2009; Yravedra, 2005) as consistently as are cut marks. Though mandibles are abundant at DK1, podial elements are not particularly well represented. Furthermore, mole-rat upper limb skeletal elements and innominates are fairly well represented, a skeletal-part pattern that differs from the part representation pattern reported in studies regarding the processing of fur-bearing mammals.

The other small mammal prey species at DK1 do not exhibit a pattern of cut marks similar to that of the mole-rats nor do they exhibit skeletal-part patterns indicative of skinning. For example, cut marks on hare, hyrax, carnivores, and size 1 bovids mostly cluster around scapula and humerus, the innominates and femurs, and vertebrae and ribs, locations indicative of disarticulation and filleting (Binford, 1981; Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003; Hill and Behrensmeyer, 1984; Nilssen, 2000; O'Connell and Hawkes, 1988; O'Connell et al, 1990) as opposed to skinning.

Taphonomic evidence of the exploitation of Cape dune mole-rats for their fur is evident in multiple strata at DK1. It is markedly apparent in LSA and MSA layers 6, 7, 10, 12, and 14 where in each case >80% of cut marks are found in anatomical locations suggestive of skinning. This pattern implies that MSA humans habitually utilized mole-rats for their fur over a prolonged period of time,

spanning the MSA occupation as well as the LSA. This pattern represents the first evidence for the habitual skinning and utilization of fur-bearing mammals by MSA humans.

In addition to their fur, MSA humans may also have used mole-rats as a food resource. Mole-rats are consumed by people today and are an important protein source for some rural populations in parts of the Western Cape Province (Henshilwood, 1997; Schweitzer, 1979). Henshilwood (1997) documented mole-rat preparation and studied the discarded remains of mole-rats consumed by modern people, observing that mole-rats are usually not skinned before being roasted over hot coals. However, this does not rule out such behavior in the past. He noted that when prepared in this way, a distinctive burning pattern in which the premaxillae, incisors, and podial bones were disproportionally burned in relation to other skeletal elements. A similar anatomical pattern of burned skeletal elements was not observed in the DK1 LSA or MSA mole-rat remains. Burned and calcined mole-rat bones are present in varying frequencies throughout the assemblage (Table 24) and a variety of skeletal elements exhibit burning. There are, however, no particular elements that are more burned than others. Further, there are some bones which are both cut-marked and burned. Many elements are completely or partially calcined, a process which requires exposure to a high degree of heat for a prolonged period of time (Stiner et al, 1995).

Implications for MSA Human Populations

The estimation of MSA population densities from archaeological evidence is challenging. Hunter-gatherer societies leave behind only ephemeral traces of their existence and only a small portion of the material they produced is likely to be preserved. In southern Africa, researchers have relied on proxy indicators of MSA human population densities such as the number of archaeological sites dated to a particular time period (Jacobs et al, 2008a; 2008b; Klein, 2001; 2008; Mellars, 2006), the intensity of site occupations (Avery et al, 2008; Faith, 2013; Karkanas et al, 2015; Parkington, 2013; Steele and Klein, 2013; Thompson, 2010b; Thompson and Henshilwood, 2011; Wadley and Jacobs, 2006), the impact of humans on specific types of resources (Clark, 2011; Halkett et al, 2003; Henshilwood et al, 2001a; Klein, 1998; 2008; Klein and Cruz-Uribe, 2000; Klein and Steele, 2013; Klein et al, 2004; Parkington, 2003; 2008; Steele and Klein, 2005/6), and evidence for (and against) the transmission of adaptive cultural innovations (Brown et al, 2012; Conard and Will, 2015; Dusseldorp, 2014; Klein, 2008; Lombard and Parsons, 2011; Mackay et al, 2014; Porraz et al, 2013a; Powell et al, 2009; Shennan, 2001).

On the southern coast of South Africa, archaeological sites dating to late MIS5 and MIS4 are abundant (Jacobs et al, 2008a; 2008b). Even though global climate conditions were cooler during MIS4, there is strong evidence for intensive

human occupations at sites such as BBC (Jacobs et al, 2006; Tribolo et al 2006), DRS (Miller et al, 2013; Parkington, 2013; Porraz et al, 2013b), PP5-6 (Brown et al, 2012; Karkanas et al, 2015), and Klasies River Mouth (Deacon, 1995; Feathers, 2002; Singer and Wymer, 1982). Humans occupying these sites appear to have ameliorated deteriorating climate conditions by exploiting a range of coastal and terrestrial resources (Clark and Kandel, 2013; Faith, 2013; Klein, 1976; Klein and Cruz-Uribe, 1996; Marean, 2014; Steele and Klein, 2013; Thompson, 2010b; Thompson and Henshilwood, 2011). In addition, evidence for adaptive cultural innovations in the forms of symbolism (Henshilwood et al, 2002; Henshilwood et al, 2004; Texier et al, 2010) and technological innovations (Brown et al, 2009; 2012; d'Errico and Henshilwood, 2007; Henshilwood et al, 2001b; Porraz et al, 2013a; Villa et al, 2010) are evident.

Some researchers have argued that these factors may reflect a broader regional shift towards larger human populations in response to the glacial conditions of MIS4 (Jacobs, 2008a; Karkanas et al, 2015; Marean et al, 2014; Mellars, 2006; Wadley et al, 2011). This pattern contrasts with the archaeological record of the previous glacial phase of MIS6 as far fewer archaeological sites in the Cape date to this period. The population expansion during MIS4 is evidenced by (1) the marked increase in the number of archaeological sites, (2) comparatively intensive human occupations at archaeological sites, and (3) increased visibility of adaptive technological and cultural innovations, suggesting that the response(s) to cooling and

environmental fluxes by MIS4 human populations diverged from those of MIS6 populations.

The demographic shift towards greater population densities may have been driven by – and/or exhibited in – human behavioral changes during MIS4 that made it possible to not only survive strenuous climate events but to thrive. These adaptive changes appear to have included a turn towards focused and intensive use of habitats as evidenced by the range of coastal and terrestrial resources exploited during this period. With the assumption that the MSA occupation at DK1 dates to MIS4, the evidence for periodic but concentrated exploitation of Cape dune mole-rats (particularly in layers MSA6, 10, 12, and 14) reflects this adaptive response by humans towards the intensive utilization of habitats as demonstrated by the exploitation of this lower-ranked resource.

The anthropogenic accumulation of higher-ranked, higher-yield resources, such as large ungulates, has been documented in MSA layers at DK1 (Marean et al, 2000a; Thompson, 2008). However, evidence for the exploitation of medium-sized ungulates is less common in these same layers (Marean et al, 2000a; Thompson, 2008), possibly as a result of local decline in abundance of these ungulates as the climate deteriorated during MIS4. Small mammals endemic to the CFR appear to have been less affected by the changing climate and environmental conditions as they are abundant at DK1 and consistently represented at other sites dated to MIS4 in the CFR. Micromorphology thin

sections from layers MSA6 and 8 at DK1 reveal shellfish – a high-ranking resource due to population densities and spatial predictability – in a state of dissolution suggesting that shellfish were once present at the site but since removed by decalcification (Goldberg, 2000). Because of their preservation state, it is difficult to deduce the intensity of shellfish utilization by MSA people at DK1. In addition to large ungulates and possibly shellfish, it seems that humans relied on small mammals – particularly mole-rats but also size 1 bovids and hares – to fill the void left locally by the decline of higher-ranked resources, namely medium-sized ungulates.

The emphasis on lower-ranked resources for sustenance and perhaps skins (supported by the pattern of cut marks on mole-rat bones) suggests that the MSA inhabitants of DK1 expanded their resource base as an adaptive response to a changing landscape. It can be surmised that high-yield habitats that featured ample hunting opportunities as well as access to coastal resources were the preferred occupation zones of hunter-gatherers during MIS4 in the CFR. However, it is likely that these high productivity habitats were infrequent on the landscape (as they are today) and elevated population densities potentially led to increased competition for these habitats. The utilization of small mammals at DK1 is evidence for the exploitation of lower-ranked resources and the maximization of habitat yield as an adaptive response to a fluctuating environment and competition for resources, a shift not previously discerned in MSA archaeofaunas.

At PP5-6, the MIS5 occupations have been described as repeated, short visits by small groups of hunter-gatherers (Karkanas et al, 2015). Geoarchaeological analysis of PP5-6 shows that the MIS4 occupations were more intense than those of MIS5, probably a reflection of more frequent and longer occupations, possibly by larger groups of people (Karkanas et al, 2015). Shellfish remains are abundant in the MIS5 and MIS4 strata at PP5-6. A taphonomic analysis of the large mammals from PP5-6 has not been reported, but there is reason to believe that large mammal hunting was an important aspect of the PP5-6 inhabitants life-ways as there is a marked shift to microlithic technology at the beginning of the climate deterioration of MIS4 (Brown et al, 2012). The microliths reported from PP5-6 resemble those typically utilized as armaments on small, long throw projectile weapons used to hunt large mammals (Brown et al, 2012).

Unlike DK1, small mammals do not seem to have been an important part of the resource base at PP5-6. In all layers, they make up only a tiny fraction of the sampled fauna and with the exception of specimens from layers NWR and LBSR, the taphonomy indicates that humans played little to no role in the accumulation of small fauna at PP5-6. Predators contributed comparatively few Cape dune mole-rats, hares, and rock hyraxes to the deposit at PP5-6, however raptors are likely responsible for many of the size 1 bovid remains recovered at the site. It is also possible that density-mediated destruction and trampling played a role in the reduction of small mammal frequencies, given the fractured

and diminished state of the specimens. Yet if small mammal remains were once present in greater numbers, one would expect to recover more than four mole-rat, nine hare, and four rock hyrax bones given their general abundance at other CFR MSA sites. The taxonomic pattern of small mammals predated on by non-human predators suggests that mole-rats, hares, and rock hyraxes may not have been particularly abundant in the immediate vicinity of PP5-6; neither predators nor humans accumulated them in any substantial way. During MIS4 humans probably focused their attention on the abundant high-quality coastal and terrestrial resources provided by access to the coastline and the large ungulates that inhabited the grassy plains adjacent to the rockshelter.

Die Kelders Cave 1 Small Mammal Discussion

The present taphonomic analysis reveals that humans and nocturnal raptors (possibly the Cape eagle-owl) played the primary roles in the accumulation of small mammals at DK1. There is very little indication of mammalian carnivore involvement in the accumulation of small mammals at the site. In general, the small mammals from even-numbered LSA and MSA layers were accumulated by humans or exhibit a mixture of human and raptor taphonomic contribution signals. The small mammals from odd layers were in large part accumulated by raptors with minimal human contribution. This depositional pattern in which anthropogenic input is most concentrated in even

numbered layers is consistent with the patterns of large mammals (Marean et al, 2000ab; Klein and Cruz-Uribe, 2000), stone tools (Thackeray, 2000), and micromorphological (Goldberg, 2000) analyses previously conducted regarding DK1.

Of the specific small mammal taxonomic aggregates, Cape dune mole-rats, size 1 bovids, and hares exhibit the strongest indications of anthropogenic accumulation. This pattern is apparent across multiple strata, with particular emphasis on layers LSA, MSA 6, 10, 12, and 14 (Fig. 27). Rock hyrax specimens show some signs of human accumulation (especially layers MSA 6 and 12) but for the most part appear to have been accumulated by raptors. Carnivores are the least-numerous SMA by NISP, show no evidence of human accumulation, and exclusively exhibit taphonomic indication of raptor accumulation.

At DK1 Cape dune mole-rats are by far the most abundant taxon, a pattern common to MSA sites in the CFR. What is unusual is the unmistakable taphonomic evidence (principally cut marks) that indicates humans played a substantial roll in the accumulation of mole-rats. Clear taphonomic evidence for mole-rats as part of the resource base of MSA humans has not been previously documented. However, anthropogenic accumulation of size 1 bovids is fairly typical at southern African MSA sites; examples include PP13b (Thompson, 2010b), BBC (Thompson and Henshilwood, 2011), Sibudu Cave (Clark and Plug,

2008; Wadley, 2010), DRS (Steele and Klein, 2013), and YFT1 (Avery et al, 2008) among others. Additionally, taphonomic support for human accumulation of rock hyraxes during the MSA has been recognized (Badenhorst et al, 2014; Cruz-Uribe and Klein, 1998), however, it is not particularly common. There is little mention in the literature of anthropogenic accumulations of hares at MSA sites in the CFR – though this may simply reflect the lack of detailed taphonomic analyses of hare archaeofaunal remains (the same may apply to rock hyraxes as well). Nevertheless, many hare remains at DK1 exhibit evidence of anthropogenic accumulation.

Given the abundance of Cape dune mole-rats at DK1 and the evidence for anthropogenic accumulation, the question arises: Were humans responsible for few, some, or most of the MSA mole-rats?

There is strong evidence for at least partial human agency of mole-rat remains in all but two of the sampled strata at DK1 (the exceptions are layer MSA 13 and 15). Layers LSA, MSA10, and MSA14 each feature substantial portions of cut-marked and burned bone (much of it calcined) and few digested or beak/talon/tooth punctured and/or pitted specimens (Table 24). The mole-rats from these layers cluster very closely with the small mammal control assemblages that were accumulated by humans (Fig. 26). It seems reasonable to conclude that the mole-rats from layers LSA, MSA10 and MSA14 were accumulated primarily by humans. The mole-rats from layers MSA6 and MSA12

exhibit sizable proportions of cut-marked and burned (much of it calcined) specimens but also include some predator digested, punctured, and/or pitted bone. Specimens from layers MSA6 and MSA12 are of mixed agency but probably favor anthropogenic accumulation given the frequency of human-induced bone surface modifications in contrast to the predator modifications. In these layers, humans probably accumulated the majority of mole-rats with raptors playing a secondary role.

The remaining layers exhibit mixed human and raptor contribution but with greater proportions of raptor introduced bone surface modifications. In layers MSA7, MSA8, MSA9, and MSA11, raptors appear to have contributed the majority of the mole-rats, and humans contributed far fewer (Fig. 5). Raptors (likely nocturnal) accumulated nearly all of the mole-rats in layers MSA13 and MSA15 given the abundance of raptor bone surface modifications and the relative lack human induced modifications. Additionally, these layers (along with MSA8 and MSA9) are among those that show the fewest signs of human accumulation across all SMAs.

Pinnacle Point Site 5-6 Small Mammal Discussion

The PP5-6 small mammal fauna contrasts with the DK1 sample in a number of ways. Small mammals are a much small portion of the mammalian fauna at PP5-6, accounting for only 4% of all mammals as opposed to 85% at

DK1. Of the identifiable small mammals at PP5-6, Cape dune-mole rats, hares, and rock hyraxes make up only a small fraction of the sampled specimens. These taxa are often a substantial portion of MSA archaeofaunas from sites in the CFR, and mole-rats in particular are typically well represented. For instance, mole-rats at DK1 are 75% of the small mammal sample by NISP but make up <2% of the small mammals at PP5-6.

The small mammal representation at PP5-6 in terms of overall proportion of the assemblage as well as representation of individual small mammal taxa is dissimilar to many other MSA sites in the CFR such as BBC, YFT1, and DRS. These sites characterize a more 'typical' pattern of faunal representation where small mammals constitute large fractions of the assemblages and where mole-rats are the most abundant small mammal taxon. PP5-6 is similar to PP13b in that there are few small mammal specimens in relation to other mammals and very few mole-rats in particular. The abundance and representation of small mammals at the Pinnacle Point sites is uncharacteristic of MSA archaeofaunas in the CFR.

The taphonomy of the small mammals at PP5-6 differs from DK1 in relation to preservation history and accumulation as they are largely not well preserved. In comparison to DK1, they are more fragmented, smaller in maximum dimension, and there are less of the original bone surfaces visible for analysis (where bone surface modifications might be preserved). Because of

these factors, comparatively fewer PP5-6 specimens are identifiable to taxon and skeletal element. Undoubtedly, preservation conditions have had an impact on the survivorship and visibility of some bone surface modifications.

However, several predator-induced bone surface modifications were preserved and these reveal that most of the PP5-6 small mammals were accumulated by raptors. Mammalian carnivores do not appear to have played a significant role in the accumulation of small mammals. Both nocturnal and diurnal raptors accumulated the bulk of the small mammals with diurnal raptors likely responsible for accumulating the majority of small mammals (Fig. 32) as evidenced by high relative frequencies of punctured and pitted small mammal bones as well as moderate relative levels of digestion. Humans played a small yet detectable role in the accumulation of faunal remains as the size 1 bovids from stratum NWR and the small mammal group from stratum LBSR exhibit evidence of human accumulation in the form of cut marked and burned bones. In addition, these specific taxonomic aggregates exhibit minimal levels of predator accumulation. Though only these two aggregates cluster with the human accumulated control samples (Fig. 10), a pocket of burned bone is apparent in stratum DBCS. However, specimens from this layer also exhibit elevated levels of beak/talon/tooth punctures and pits, suggesting a more complex accumulation history and one that favors raptor accumulation and where humans played a secondary role.

In comparison to DK1, the small mammal taphonomy at PP5-6 exhibits nominal evidence for human accumulation. The diminished relative frequencies of human-induced bone surface modifications and the proportion of small to large mammalian fauna suggests that small mammals were not an important part of the resource base for MSA humans at PP5-6 as they were at DK1.

CONCLUSIONS

The above taphonomic analysis demonstrates that humans played a central role in the accumulation of MSA small mammal archaeofaunas at DK1. The analysis also confirms that nocturnal raptors were a leading contributor to the DK1 small mammal accumulations as well. Humans were frequently the primary accumulators of Cape dune mole-rats as well as hares and size 1 bovids in strata that are probably MIS4 in origin while nocturnal raptors were likely responsible for the small mammals not accumulated by humans. The majority of cut marks on mole-rat bones are found at anatomical locations indicative of skinning and are interpreted as such. Mole-rat remains also show evidence of intentional burning, some specimens are both cut-marked and burned, suggesting that they may have been roasted on a fire and utilized as a food source in addition to being skinned. This analysis constitutes the first evidence for the habitual utilization of mole-rats and for skinning of small, fur-bearing mammals during the MSA of southern Africa.

The MSA occupations at PP5-6 do not show the same concentrations of small mammal accumulations by humans. The taxonomic composition, relative abundancies, and taphonomic profiles of the PP5-6 small mammals differ from those of DK1 indicating that small mammals were not an important part of the resource base of humans at PP5-6 during late MIS5 and MIS4. Concentrations of shellfish and microlithic stone tools, suggest that humans were concentrating their subsistence efforts on high-quality resources, probably in response to the high-yield habitats in the vicinity of PP5-6. Additionally, most of the PP5-6 sample was accumulated by diurnal and nocturnal raptors but few of the prey species found in great numbers at DK1 (i.e. mole-rats, hares, and hyraxes) and other sites in the CFR were recovered in abundance at PP5-6 indicating that these species may have been less prevalent on the landscape near PP5-6 or represented a less-preferable option to humans and predators.

The analysis presented here provides the first comprehensive taphonomic study of small mammals from southern African MSA archaeological sites and demonstrates that taphonomic studies can be used to address aspects of human behavior during this critical time period in human evolution. It is clear that humans utilized a range of resources and protein sources during the MSA and that small, fur-bearing mammals were at times an important resource at DK1. Small mammals, however, were not a significant resource for the contemporaneous humans who occupied PP5-6. This difference in subsistence strategies suggests that the adaptive response of MIS4 humans to glacial

conditions and resultant habitat fluctuations was to maximize their resource base and exploiting lower-quality resources when necessary. The increased visibility of MIS4 archaeological sites in the Cape suggests that human population densities were greater and that these humans responded differently than previous populations did to glacial conditions. The flexibility to incorporate new resources into their subsistence base may have been one of the behavioral differences that allowed MIS4 human populations to thrive.

DISSERTATION CONCLUSION

This dissertation began as an attempt to address the disparity in our knowledge concerning the role of small mammal resources in the economies of MSA humans in South Africa's Cape Floristic Region. To accomplish this, the Die Kelders Cave 1 and Pinnacle Point site 5-6 assemblages were selected for study as the sites were contemporaneously occupied by humans and spatially distinct. However, in order to accurately assess the DK1 and PP5-6 archaeofaunas, it was necessary to address some of the limitations of present taphonomic methods and refine techniques concerning the attribution of small mammal accumulators, namely humans, mammalian carnivores, and raptors. In so doing, these broader questions were addressed: Were humans responsible for the accumulation of small mammals at MSA sites in South Africa? If so, why were these resources targeted over others? Were small mammals an important component of the diet? Did diet breadth increase during the South African MSA?

Paper 1 addressed the taphonomy and composition of prey remains accumulated by Verreaux's eagles, a raptor which nests in or around rockshelters and cave mouths, places that attract other bone accumulators, including humans. It is evident that Verreaux's eagle is a major accumulator of small mammals, often specializing on rock hyraxes. It also appears that there is a correlation between local availability of mammalian prey and prey selectivity by the eagle as the proportion of rock hyraxes in the diet fluctuates between 40-90%

and is supplemented with other locally-available mammals. This study found that hares, mole-rats, small bovids, and small carnivores – in addition to rock hyraxes – constitute the majority of prey in the eagle's diet in the Cape Floristic Region.

Based on the form and frequency of bone modifications observed in the study, it is evident that Verreaux's eagle causes more damage to the bones of their prey in comparison to other eagle species. For instance, broken and punctured specimens were commonly observed bone surface modifications. These modifications are less common among other eagles' (such as bald, marshal, and imperial eagles) prey accumulations. The frequency of damage inflicted by Verreaux's eagle indicates that there is taphonomic variability in the ways that different eagle taxa process and accumulate their prey. In short, there is not a "one size fits all" modification pattern for eagles. Taphonomic patterns derived from predation by other eagle taxa are not the appropriate general proxies from which to identify Verreaux's eagle predation.

There is, however, patterned variability in the ways Verreaux's eagle accumulates and modifies bones. In paper 1 there were two distinct skeletal-parts preservation, bone breakage, and bone surface modification patterns: one that characterizes rock hyraxes, mole-rats, and carnivores, and another that characterizes hares and bovids. Faunal analysts investigating the potential role of Verreaux's eagle at fossil sites should be aware of these taphonomic patterns and that there is no singular pattern of accumulation, especially with regard to

skeletal-part preservation. However, there are patterns of preservation, breakage, and bone modification that can be employed on a taxon-specific basis to differentiate Verreaux's eagle prey remains from those of other bone accumulators. These include a puncture frequency of approximately 10% and bone fracture rates >10% for all taxa. There are also elevated levels of preservation for crania and mandibles (except of hare) in comparison to other predators.

Paper 2 provided a comprehensive taphonomic assessment of rabbits and guinea pigs accumulated by a bald eagle, great horned owl, and coyote. The study revealed taphonomic differences between these diverse small mammal accumulators as well as variation between prey of different sizes. Small mammal actualistic and experimental taphonomic studies often feature leporids as the prey species; however, this analysis also features guinea pigs, a prey taxon of different size and build, augmenting the range of actualistic and experimental small mammal taphonomic studies.

Paper 2 indicated that there is substantial taphonomic variation between rabbits and guinea pigs modified by the three predators. These predators produced significantly different intraspecific rabbit- and guinea pig-ingested and non-ingested skeletal-part profiles where the predators ingested far more guinea pig remains. The bald eagle and coyote produced significantly different intraspecific deleted-part profiles, while the bald eagle and great horned owl

generated significantly different intraspecific non-ingested fragmented-part profiles. In addition, the interspecific predator-part profile comparisons are, with few exceptions, dissimilar.

The intra- and interspecific predator bone surface modification comparisons reveal a mixture of relationships underlining the differences between the predators and prey taxa. Some modification frequencies are not significantly different, namely notch and score frequency. However, punctures, pits, digested, crenulated, and fractured-edge specimens reveal a combination of significant and non-significant intra- and interspecific predator comparisons. There are tangible surface modification differences between the samples, further demonstrating that the predators handle small prey of different sizes and builds distinctively. Further, it is possible to distinguish between the small prey samples by predator with the combined suite of bone surface modification frequencies and -part profiles.

Taphonomic comparisons between this study and other diurnal raptor small mammal analyses reveal a high degree of variability in terms of ingested and non-ingested skeletal-part profiles, bone fragmentation, and surface modifications. It seems that different eagle taxa create a wide range of taphonomic variation even when only leporids are considered. The great horned owl assemblages share more in common with other nocturnal raptor prey accumulations, particularly fragmentation and surface modification frequency,

and to a lesser extent skeletal-part frequencies. The coyote assemblages are taphonomically similar to other published medium carnivore accumulated assemblages, but surprisingly different than some fox-accumulated leporid collections.

Unfortunately there were very few assemblages to which the guinea pig samples could be compared. The comparisons reveal the range in variability, but also the similarities, among the small mammal taphonomic analyses, emphasizing the need for a wider assortment of small mammal predator and prey taphonomic studies.

Based on the results of papers 1 and 2, the implication for faunal analysts is that variability in small mammal assemblages is introduced by both predator and prey type. The taphonomic profile of leporids accumulated by a particular predator taxon may not match the profile of guinea pig-sized prey collected by the same predator. Therefore taphonomic patterns derived from predation on leporids by diurnal and nocturnal raptors and carnivores may not offer the appropriate proxies for the identification of predation on other prey taxa by these same predators.

Expanding the base of experimental and actualistic studies to included predation on non-leporid small mammals will help provide the proxies necessary to identify the origin of small mammal accumulations. As many archaeological assemblages feature a mixture of accumulators, the analysis of raptor and

mammalian carnivore predation on rabbits and guinea pigs presented in this study will help differentiate predation between these predators and humans in archaeological assemblages.

Paper 3 demonstrates that humans played a central role in the accumulation of MSA small mammal archaeofaunas at DK1 but that nocturnal raptors were also an important contributor of small mammals at the site. Humans were frequently the primary accumulators of Cape dune mole-rats as well as hares and size 1 bovids in strata that are probably MIS4 in origin while nocturnal raptors were likely responsible for the small mammals not accumulated by humans. Most of the cut marks on mole-rat bones were found at anatomical locations indicative of skinning, suggesting that MSA humans habitually utilized mole-rats for their furs. Mole-rat remains also show evidence of intentional burning, some specimens are both cut-marked and burned, indicating that they may have been roasted on a fire and utilized as a food source in addition to being skinned.

The MSA occupations at PP5-6 do not show the same concentrations of small mammal accumulations by humans. The taxonomic composition, relative abundancies, and taphonomic profiles of the PP5-6 small mammals differ from those of DK1, indicating that small mammals were not an important part of the resource base of humans at PP5-6 during late MIS5 and MIS4. Concentrations of shellfish and microlithic stone tools, suggest that humans were concentrating

their subsistence efforts on high-quality resources, probably in response to the high-yield habitats in the vicinity of PP5-6. Additionally, most of the PP5-6 sample was accumulated by diurnal and nocturnal raptors but few of the prey species found in great numbers at DK1 (i.e. mole-rats, hares, and hyraxes) and other sites in the CFR were recovered in abundance at PP5-6. This suggests that these species may have been less prevalent on the landscape near the site, or represented a less-preferable option to humans and other predators.

The analysis presented in paper 3 provides the first comprehensive taphonomic study of small mammals from southern African MSA archaeological sites and demonstrates that taphonomic studies can be used to address aspects of human behavior during this critical time period in human evolution. It is clear that humans utilized a range of resources and protein sources during the MSA and that small, fur-bearing mammals were at times an important resource at DK1. Small mammals, however, were not a significant resource for the contemporaneous humans who occupied PP5-6. This difference in subsistence strategies suggests adaptive response by MIS4 humans to glacial conditions and resultant habitat fluctuations in order to maximize their resource base and exploit lower-quality resources when necessary. The increased visibility of MIS4 archaeological sites in the Cape suggests that human population densities were greater and that these humans responded differently than previous populations to glacial conditions. The flexibility to incorporate new resources into their

subsistence base may have been one of the behavioral differences that allowed MIS4 human populations to thrive.

The origins of the ‘modern human behavioral’ repertoire, in terms of the timing and conditions in which this suite of behaviors evolved, continues to be an active and growing subject and remains at the center of MSA research in southern Africa. Though new archaeological discoveries, analyses, and debates are continuously shaping our understanding of the ‘modern human behavioral’ repertoire, adaptable foraging strategies and use of landscapes by MSA humans remains a core component of this research and of our understanding of human behavioral complexity. Different methodological and epistemological approaches to examining foraging and landscape utilization strategies continue to expose new aspects of MSA human lifeways. This dissertation introduces new data and analyses that modify our understanding of MSA human resource utilization strategies in relation to small mammals, protein procurement, the use of fur-bearing mammals, and adaptations to environmental and population changes during the MSA of southern Africa.

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APPENDIX A:

Acronyms used in this dissertation

AN = Anterior

AP = Appendicular

AX = Axial

BBC = Blombos Cave

BP = Before Present

C = Crania

CFR = Cape Floristic Region

DK1 = Die Kelders Cave 1

DRS = Diepkloof Rockshelter

ESR = Electron Spin Resonance

GP = Guinea pig

HP = Howiesons Poort

LSA = Later Stone Age

MAU = Minimum Animal Unit

MIS = Marine Isotope Stage

MNE = Minimum Number of Elements

MNI = Minimum Number of Individuals

MSA = Middle Stone Age

NISP = Number of Identified Specimens

PC = Post Crania

PO = Posterior

OSL = Optically Stimulated Luminescence

PP5-6 = Pinnacle Point Site 5-6

PP13b = Pinnacle Point 13b

SMA = Small Mammal Analytical Aggregates

ST = Stylopodium

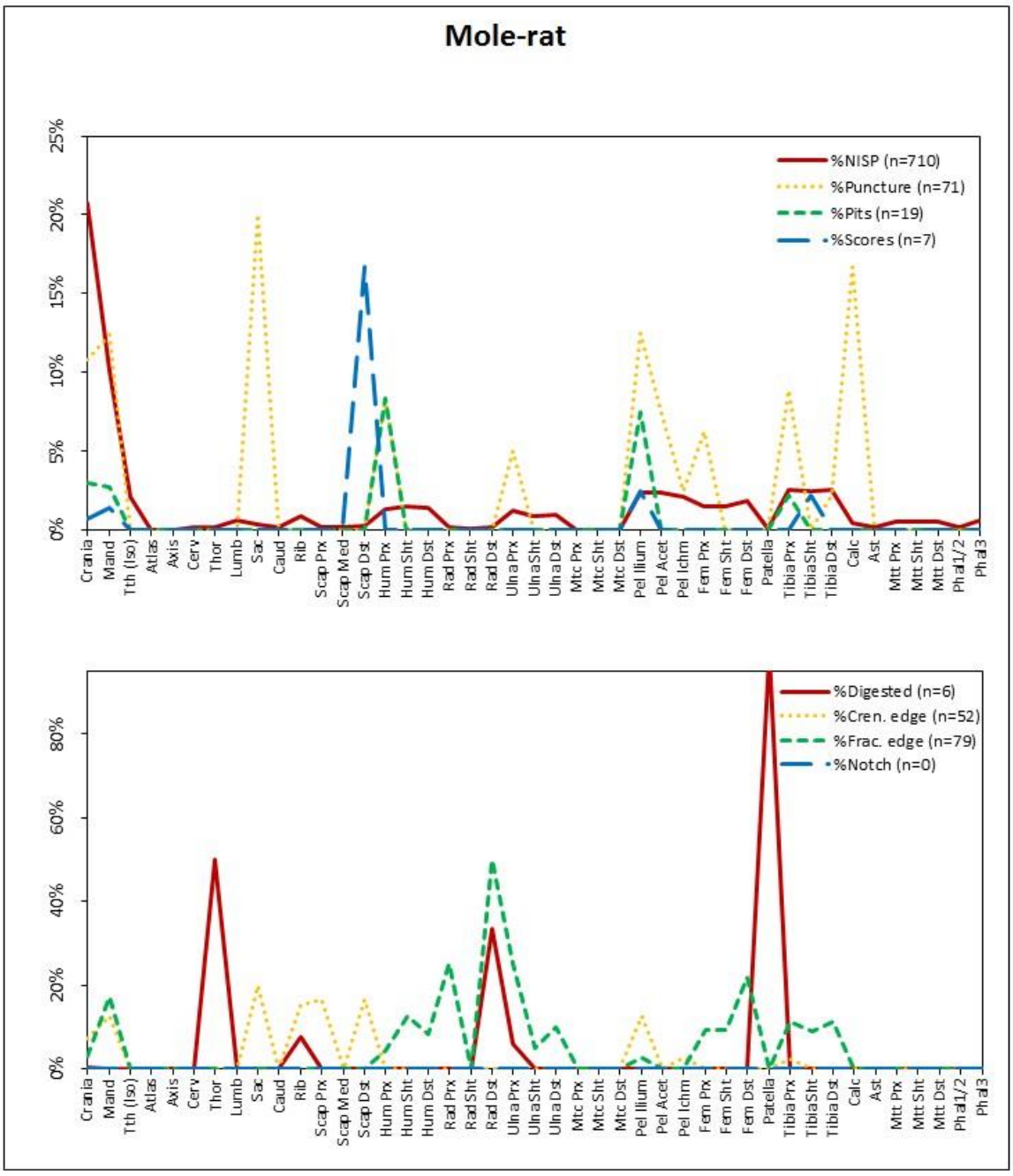
YFT1 = Ysterfontein 1

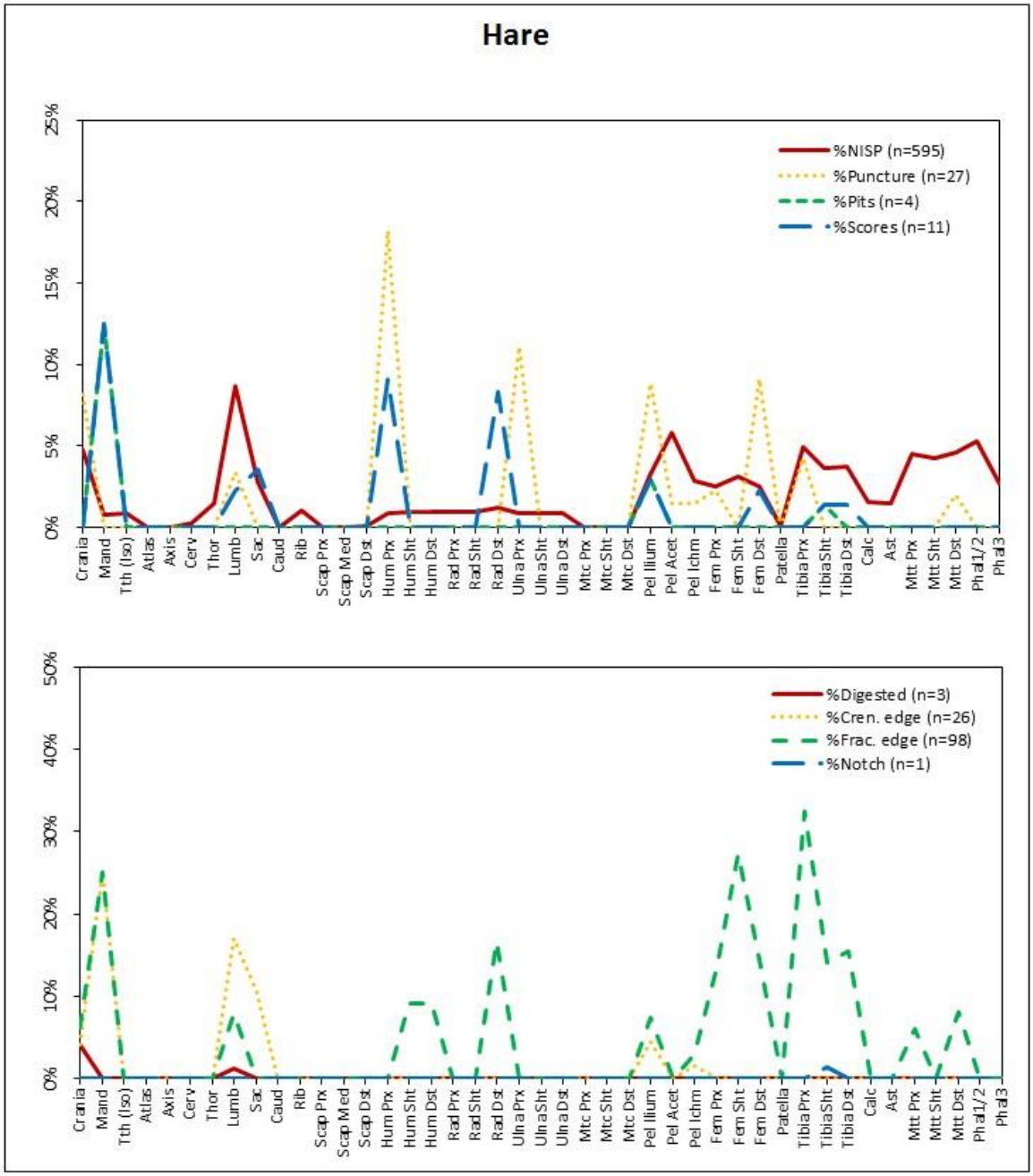
VE = Verreaux’s eagle

ZE = Zygopodium

APPENDIX B:

Percent frequency of bone surface modifications in the Verreaux's eagle samples by skeletal element for each prey aggregate. There are two graphs for each prey aggregate: the upper graphs show percent NISP, punctures, pits, and scores; the lower graphs show percent digested, crenulated edges, fracture edges, and notches.

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%Scores (n=11)
%Digested (n=3)
%Cren. edge (n=26)
%Frac. edge (n=98)
%Notch (n=1)
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5%
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20%
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Crania
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Atlas
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Cerv
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Rib
Scap Prx
Scap Med
Scap Dst
Hum Prx
Hum Sht
Hum Dst
Rad Prx
Rad Sht
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Mtc Prx
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Mtc Dst
Pel Ilium
Pel Acet
Pel Ichm
Fem Prx
Fem Sht
Fem Dst
Patella
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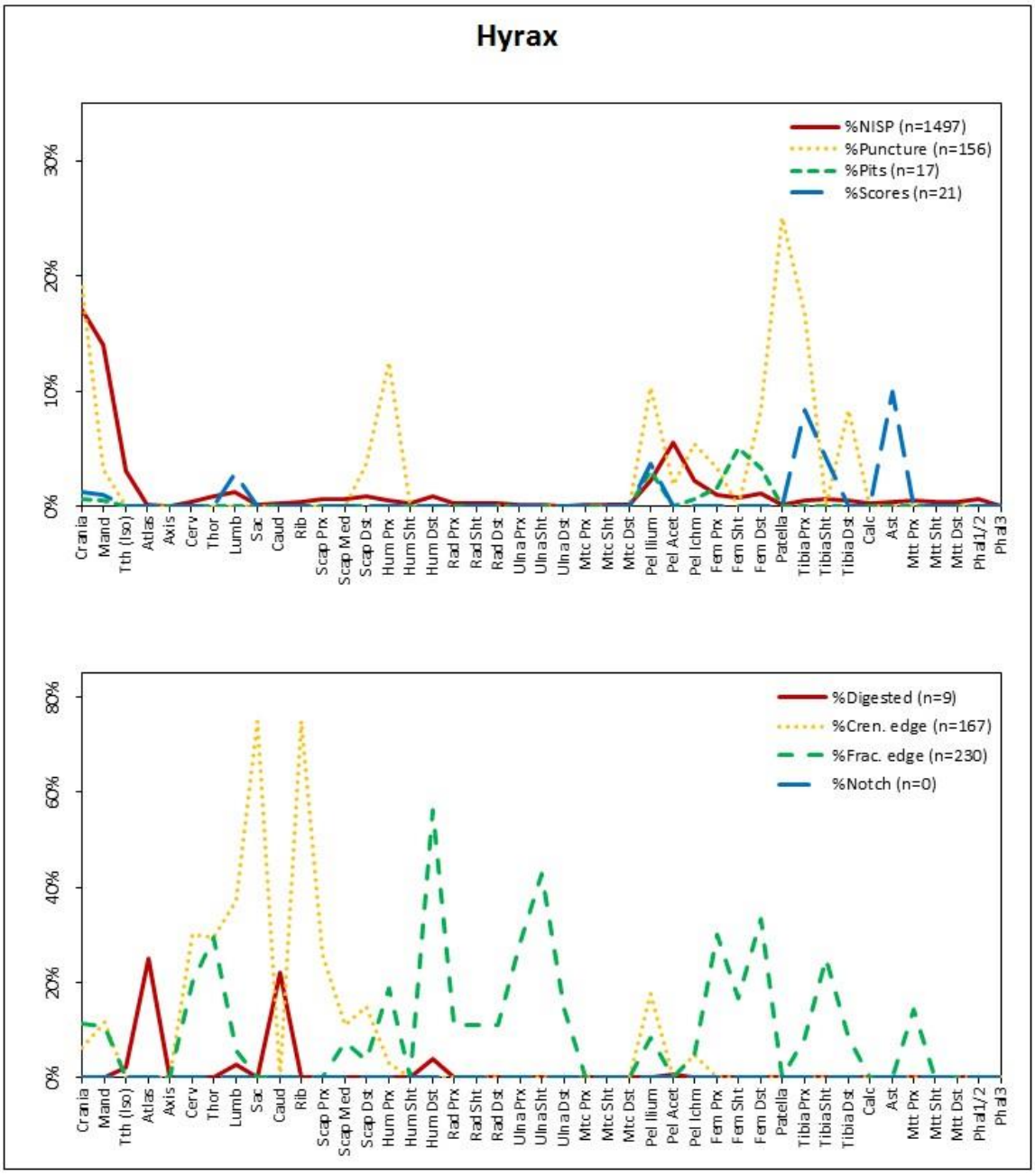
Phal1/2
Phal3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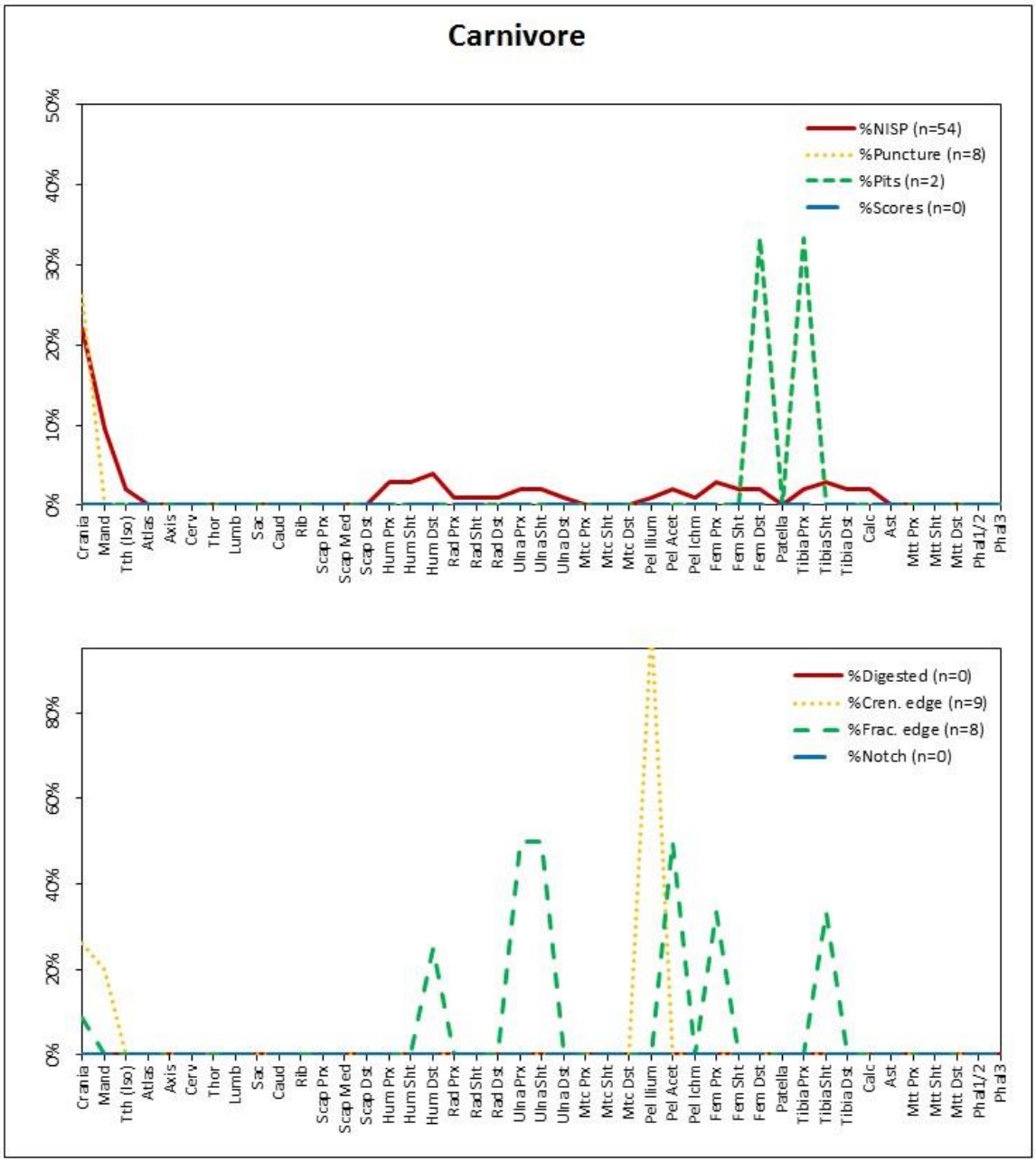
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Pel Ilium
Pel Acet
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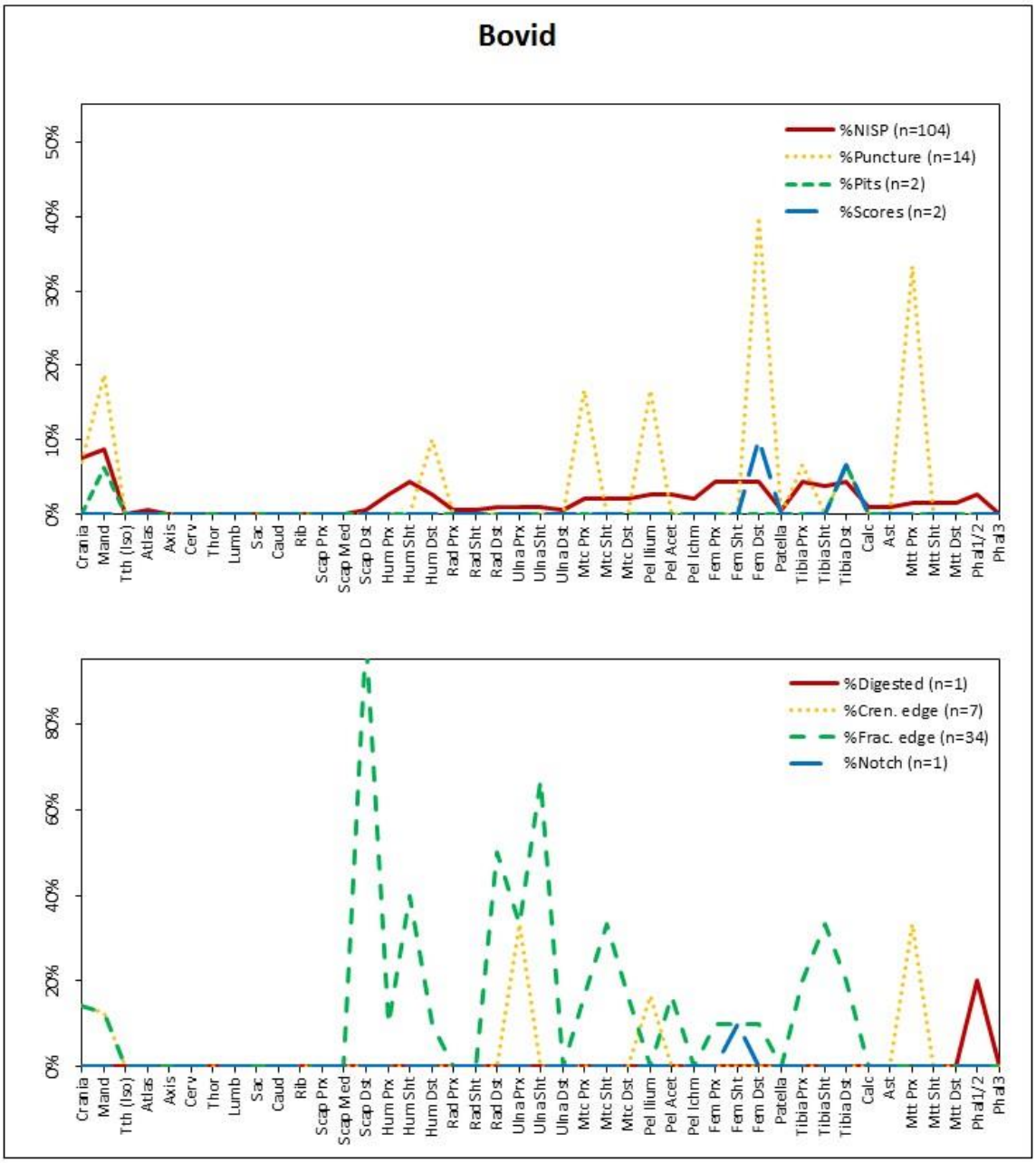
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Mtc Dst
Pel Ilium
Pel Acet
Pel Ichm
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Fem Sht
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80%

APPENDIX C:

Skeletal-part representation, fragmentation, digestion, and beak/tooth puncture comparisons between small mammal remains from digested (pellets & scats) and undigested (surface & nest) diurnal and nocturnal raptors and carnivores.

1. Armstrong & Avery; 2. Cruz-Uribe & Klein, 1998; 3. McGraw et al., 2006; 4. Sanders et al., 2003; 5. Trapani et al., 2006; 6. Lloveras et al., 2008a; 7. Hockett, 1991; 8. Hockett, 1995; 9. Sanchis Serra, 2000; 10. Lloveras et al., 2009; 11. Cochard, 2004; 12. Hockett & Haws, 2002; 13. Hockett, 1999; 14. Lloveras et al., 2008b; 15. Rodriquez-Hidalgo et al., 2013; 16. Schmitt & Juell, 1994.
n/r = not reported
"A. Fragmentation" based on all reported NISP and MNE values
"B. Fragmentation" based on the most commonly reported NISP and MNE values: maxilla, mandible, scapula, humerus, radius, ulna, pelvis, femur, and tibia

Predator	**Diurnal raptors** Verreaux's Eagle *(Aquila verreauxii)*										
Origin	Pellets	Pellets	Pellets	Surface	Surface	Surface	Surface	Surface	Pellet & surface	Surface	Surface
Prey	Leporid[1] %RA	Hyrax[1] %RA	rat[1] %RA	Leporid[1] %RA	Hyrax[1] %RA	rat[1] %RA	Carn.[1] %RA	Bovid[1] %RA	Total[1] %RA	Hyrax[2] %MNI	Leporid[2] %MNI
Maxilla (Crania)	0.50	0.50	0.50	0.14	0.91	0.97	0.79	0.11	0.82	1.00	0.23
Mandible	0.00	0.00	0.00	0.03	0.97	0.52	0.36	0.46	0.70	0.81	0.10
Teeth	0.00	0.06	0.00	0.01	0.01	0.01	0.01	0.00	0.01	-	-
Vertebrae total	0.00	0.13	0.00	0.11	0.01	0.00	0.00	0.07	0.02	0.00	0.45
Sacrum	0.00	0.00	0.00	0.56	0.02	0.03	0.00	0.00	0.07	0.02	0.62
Ribs	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.01	0.00	0.01	0.00
Scapula	0.00	0.00	0.00	0.01	0.07	0.01	0.00	0.04	0.04	0.04	0.16
Humerus	0.00	0.00	0.00	0.14	0.07	0.09	0.14	0.18	0.09	0.06	0.25
Radius	0.00	0.00	0.50	0.17	0.02	0.01	0.04	0.07	0.03	0.01	0.12
Ulna	0.00	0.00	0.50	0.13	0.01	0.07	0.07	0.07	0.05	0.02	0.07
Pelvis	0.00	0.00	0.00	0.82	0.42	0.16	0.07	0.18	0.36	0.19	1.00
Femur	0.00	0.00	0.00	0.36	0.08	0.12	0.11	0.29	0.13	0.10	0.55
Patella	0.00	0.00	0.50	0.01	0.01	0.00	0.00	0.04	0.01	0.01	0.00
Tibia	0.00	0.00	0.00	0.74	0.04	0.17	0.11	0.29	0.16	0.05	0.95
Fibula	0.00	0.00	0.00	0.00	0.02	0.00	0.04	0.07	0.01	0.00	-
Calcan	0.00	0.00	0.00	0.22	0.02	0.03	0.07	0.07	0.05	0.00	0.45
Astrag	0.00	0.00	0.00	0.21	0.03	0.01	0.00	0.07	0.04	0.00	0.30
Carpals/tarsals	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-
Phal total	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.01	0.01	-	-
Metapodial tot.	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.13	0.01	-	-
NISP total	2	7	5	593	1490	705	54	104	2960	n/r	n/r
MNE total	1	7	5	480	1240	538	52	71	2394	n/r	n/r
MNI	1	1	1	36	192	107	14	14	366	3487	31
A. Fragmentation (NISP/MNE)	2.00	1.00	1.00	1.24	1.20	1.31	1.04	1.46	1.23	n/r	n/r
B. Fragmentation (NISP/MNE)	2.00	1.00	1.00	1.51	1.23	1.34	1.04	1.64	1.30	n/r	n/r
% Complete long bones	-	-	0.0	60.5	45.5	70.4	78.6	62.5	63.5	n/r	n/r
% Complete all bones	0.0	57.1	20.0	63.9	52.4	47.7	79.2	53.5	54.1	n/r	n/r
% Beak/teeth punctures	0.0	0.0	0.0	4.6	10.5	10.1	15.0	13.0	9.3	n/r	n/r
% Digested	100.0	100.0	100.0	0.2	0.0	0.0	0.0	0.0	0.6	n/r	n/r

Martial Eagle *(Polemaetus bellicosus)*		African Crowned Eagle *(Stephanoaetus coronatus)*				Spanish Imperia *(Aquila adalberti)*	Northern Harri *(Circus cyaneus)*	Golden Eagle *(Aquila chrysaetos)*	Prairie Falcon *(Falco mexicanus)*
Surface Hyrax[2] %MNI	Surface Leporid[2] %MNI	Surface Hyrax[2] %MNI	Surface Primate[3] %RA	Surface Primate[4] %RA	Surface Redtail[5] %RA	Pellets Leporid[6] %RA	Pellets Leporid[7] %MAU	Surface Leporid[8] %MAU	Surface Leporid[8] %MAU
0.98	0.00	1.00	0.26	0.49	0.55	0.44	0.00	0.06	0.19
1.00	0.00	0.81	0.1	0.1	0.1	0.34	1.00	0.00	0.42
-	-	-	-	-	-	0.43	0.00	0.00	-
0.00	0.38	0.00	0.02	0.0	0.04	0.06	0.00	-	-
0.00	0.55	0.00	0.05	0.0	0.03	-	0.00	0.47	0.38
0.00	0.00	0.00	0.01	0.0	0.01	0.02	-	-	-
0.00	0.01	0.12	0.1	0.2	0.14	0.16	0.85	0.06	0.08
0.10	0.04	0.04	0.15	0.1	0.06	0.16	1.00	0.09	0.54
0.05	0.04	0.00	0.08	0.1	0.05	0.03	0.85	0.18	0.38
0.11	0.06	0.00	0.125	0.0	0.05	0.25	1.00	0.18	0.38
0.60	1.00	0.22	0.06	0.1	0.07	0.06	0.08	0.26	0.46
0.40	0.60	0.03	0.25	0.4	0.28	0.03	0.08	0.44	0.42
0.04	0.00	0.00	-	0.0	0.02	0.22	-	-	-
0.32	0.95	0.05	0.2	0.25	0.21	0.50	0.08	0.94	1.00
0.00	-	0.00	0.15	0.2	0.2	-	-	-	-
0.03	0.43	0.00	-	0.1	0.1	0.41	0.00	1.00	0.69
0.03	0.41	0.00	-	0.0	0.0	0.19	0.00	0.97	0.65
-	-	-	-	0.0	0.0	0.05	-	-	-
-	-	-	-	0.0	0.0	0.46	0.00	-	-
-	-	-	0.01	0.0	0.0	0.09	0.00	-	-
n/r	n/r	n/r	669	413	559	824	65	156	165
n/r	n/r	n/r	n/r	n/r	545	737	64	150	141
70	75	678	204	68	103	16	n/r	n/r	n/r
n/r	n/r	n/r	n/r	n/r	1.03	1.12	1.02	1.04	1.17
n/r	n/r	n/r	n/r	n/r	n/r	1.66	1.02	1.08	1.24
n/r	n/r	n/r	61.0	n/r	58.0	0.0	72.5	n/r	n/r
n/r	n/r	n/r	41.0	n/r	61.0	27.9	n/r	n/r	n/r
n/r	n/r	n/r	n/r	n/r	n/r	n/r	n/r	1.0-2.0	1.0-2.0
n/r	n/r	n/r	n/r	n/r	n/r	98.0	n/r	n/r	n/r

Nocturnal raptors					**Carnivores**						
Eurasian Eagle-Owl			Barn Owl	Great Horned Owl	Red Fox		Red Fox &/or Iberian Lynx		Iberian lynx		Coyote
(Bubo bubo)			*alba)*	*(Bubo virginianus)*	*(Vulpes vulpes)*		*(Vulpes vulpes) (Lynx pardinus)*		*(Lynx pardinus)*		*(Canis latrans)*
Pellets & surface Leporid[9] %MNI	Pellets & surface Leporid[1] %RA	Pellets & surface Leporid[1] %RA	Pellets Leporid[5] %MAU	Pellets Leporid[5] %MAU	Scat & surface Leporid[9] %MNI	Surface Leporid[11] %RA	Surface Leporid[12] ?%RA?	Surface Leporid[13] %RA	Scat Leporid[14] %RA	Surface Leporid[15] %RA	Scat Leporids[16] ?%MAU?
0.28	0.47	0.31	0.66	0.41	-	0.08	0.56	0.29	0.64	0.51	-
0.32	0.24	0.42	0.83	0.55	-	0.50	0.39	0.48	0.82	0.41	1.00
-	0.21	0.27	-	-	-	0.25	-	-	0.77	0.36	-
0.23	0.35	0.22	-	-	-	0.05	2.9	0.22	0.17	0.17	-
0.47	-	-	0.26	0.50	-	0.16	0.11	0.19	-	-	-
-	0.29	0.36	-	-	-	0.05	-	0.04	0.18	0.16	-
0.29	0.16	0.12	0.57	0.59	-	0.29	0.11	0.19	0.54	0.08	0.40
0.54	0.34	0.23	1.00	0.66	-	0.53	0.28	0.33	0.57	0.22	0.37
0.35	0.32	0.10	0.43	1.00	-	0.32	0	0.25	0.43	0.75	0.37
0.46	0.24	0.23	0.88	0.73	-	0.63	0.17	0.31	0.61	0.66	0.50
0.75	0.90	0.63	0.46	0.82	-	0.95	1	0.73	0.61	0.90	0.33
0.81	0.90	0.54	0.56	0.50	-	0.42	0.67	0.67	0.64	0.36	0.63
-	0.95	0.62	-	-	-	0.00	-	0.04	0.43	0.01	-
0.56	0.68	0.63	0.51	0.48	-	0.63	0.89	1.00	0.43	1.00	0.23
-	-	-	-	-	-	-	-	-	-	-	-
0.37	0.92	0.92	0.92	0.52	-	0.53	-	0.60	0.39	1.00	-
0.22	0.71	0.56	0.40	0.27	-	0.47	-	0.27	0.25	0.91	-
-	0.18	0.11	-	-	-	0.11	-	0.69	0.16	0.45	-
-	0.41	0.21	-	-	-	0.11	-	0.10	0.42	0.46	-
-	0.37	0.36	-	-	-	0.38	-	0.20	0.35	0.69	-
6454	1794	1926	1639	418	10009	743	76	739	1515	8772	840
n/r	1269	1370	1146	298	n/r	632	72	726	1105	8567	480
222	19	26	n/r	n/r	15	19	n/r	26	14	107	n/r
n/r	1.41	1.41	1.43	1.40	n/r	1.18	1.06	1.02	1.37	1.02	1.75
n/r	2.22	2.87	1.54	1.48	n/r	1.42	n/r	1.06	2.22	1.17	n/r
48.0	14.6	10.8	n/r	n/r	18.6	45.4	n/r	n/r	2.5	39.4	0
49.5	53.9	45.9	n/r	n/r	36.9	65.0	n/r	n/r	43.0	77.8	7.1
present	2.0	1.3	1.4	1.0	present	6.5	24.0	8.8	0.3	0.9	0.1
~50.0	68.8	65.6	n/r	n/r	>50.0	12.4	n/r	n/r	97.2	0	100.0

APPENDIX D:

Bone fragmentation totals for ingested and non-ingested rabbit and guinea pig remains after Lloveras et al 2008).

	Bald Eagle														Great Horned Owl												Coyote											
	Rabbit							Guinea Pig							Rabbit							Guinea Pig						Rabbit							Guinea Pig					
	C	PE	PES	S	SDE	DE		C	PE	PES	S	SDE	DE		C	PE	PES	S	SDE	DE		C	PE	PES	S	SDE	DE		C	PE	PES	S	SDE	DE		C	PE	PES	S	SDE	DE
Humerus[1]	19	0	2	3	2	1		9	0	1	1	1	0		13	0	0	0	2	0		5	0	0	0	2	0		0	0	0	0	0	0		0	0	0	0	0	0
Humerus[2]	0	1	2	0	2	0		0	3	2	0	1	5		0	5	2	1	2	4		1	2	4	4	4	8		0	12	6	36	7	18		1	5	11	12	10	9
Radius[1]	17	0	0	0	0	0		10	0	1	0	2	0		13	0	0	0	1	0		7	0	0	0	0	0		0	0	0	0	2	0		0	0	0	0	0	0
Radius[2]	0	0	2	1	1	1		0	4	1	0	3	3		0	4	3	0	0	5		0	8	3	2	3	6		0	1	16	6	15	0		0	3	7	3	4	9
Ulna[1]	18	0	0	0	0	0		9	0	2	0	1	1		14	0	0	0	0	0		6	0	1	0	0	0		0	0	0	0	2	0		0	0	0	0	0	0
Ulna[2]	0	1	2	0	0	1		0	3	6	0	0	2		0	4	3	0	0	5		0	1	12	1	1	4		0	7	11	5	8	2		0	7	7	2	0	5
Femur[1]	18	0	1	0	1	0		13	0	3	1	2	1		17	1	1	3	0	1		9	0	6	1	2	3		0	0	0	0	0	0		0	0	0	0	0	0
Femur[2]	0	0	0	0	0	0		0	1	1	3	1	2		0	1	1	2	0	2		0	3	2	3	2	3		0	12	6	28	5	12		0	1	14	18	8	11
Tibia[1]	18	1	2	1	0	1		14	0	3	1	3	0		18	0	0	0	0	0		11	0	0	0	1	0		0	0	0	6	6	0		0	0	0	0	0	0
Tibia[2]	0	0	0	0	0	0		0	4	1	3	1	2		0	0	2	1	1	1		0	6	2	4	6	2		0	17	1	27	1	15		0	5	4	14	7	7
Metcarp[1]	90	0	0	0	0	0		48	0	0	0	0	0		65	0	0	0	0	0		28	0	0	0	0	0		25	0	0	0	0	0		0	0	0	0	0	0
Metcarp[2]	8	2	0	0	2	0		25	1	5	0	4	2		27	0	7	2	7	2		45	0	5	0	0	5		25	6	21	5	24	8		47	3	26	6	24	5
Metata1[1]	80	0	0	0	0	0		54	0	0	0	0	0		64	0	0	0	0	0		36	0	0	0	0	0		24	0	0	0	0	0		12	0	0	0	0	0
Metata1[2]	0	0	0	0	0	0		2	0	1	1	2	1		10	0	4	2	4	0		22	0	3	1	0	2		21	3	17	19	14	11		35	2	13	0	14	3
	C	IB	IBM	M	ZA	NC		C	IB	IBM	M	ZA	NC		C	IB	IBM	M	ZA	NC		C	IB	IBM	M	ZA	NC		C	IB	IBM	M	ZA	NC		C	IB	IBM	M	ZA	NC
Cranium[1]	5	6	14	0	3	7		2	3	4	2	0	4		2	0	12	5	2	3		1	0	12	6	3	2		0	0	1	0	1	10		0	0	0	0	0	0
Cranium[2]	0	0	0	0	0	5		0	1	11	3	1	1		0	8	4	23	7	38		0	9	2	14	2	9		0	17	0	35	18	70		0	19	11	22	20	19
	C	IP	MBI	MB	MBB	CP		C	IP	MBI	MB	MBB	CP		C	IP	MBI	MB	MBB	CP		C	IP	MBI	MB	MBB	CP		C	IP	MBI	MB	MBB	CP		C	IP	MBI	MB	MBB	CP
Mandible[1]	10	2	5	3	6	1		2	3	2	1	0	2		7	0	1	2	0	2		9	0	7	0	0	0		0	0	2	0	0	2		0	0	0	0	0	0
Mandible[2]	0	0	4	0	0	0		0	1	9	1	2	1		0	2	12	5	12	15		0	0	7	3	4	3		0	21	0	45	0	27		1	6	16	10	6	25
	C	GC	GCN	NF	F			C	GC	GCN	NF	F			C	GC	GCN	NF	F			C	GC	GCN	NF	F			C	GC	GCN	NF	F			C	GC	GCN	NF	F	
Scapula[1]	1	11	11	7	0			0	2	9	3	5			2	9	5	2	6			0	0	6	2	5			0	0	0	0	0			0	0	0	0	0	
Scapula[2]	0	2	2	1	3			0	7	0	2	2			0	4	9	29	46			0	9	7	14	21			0	10	8	6	4			0	7	7	8	14	
	C	A	AIS	AISIL	AIL	IS	IL	C	A	AIS	AISIL	AIL	IS	IL	C	A	AIS	AISIL	AIL	IS	IL	C	A	AIS	AISIL	AIL	IS	IL	C	A	AIS	AISIL	AIL	IS	IL	C	A	AIS	AISIL	AIL	IS	IL
Pelvis[1]	4	0	0	16	0	0	0	2	0	1	11	3	1	3	3	4	11	2	2	0	3	2	2	14	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pelvis[2]	0	0	0	0	0	0	1	0	1	2	0	1	0	3	0	0	1	0	0	0	0	0	1	2	0	0	1	2	0	8	5	0	9	18	27	0	3	7	3	9	13	16
	C	VB	VE	SP	LP			C	VB	VE	SP	LP			C	VB	VE	SP	LP			C	VB	VE	SP	LP			C	VB	VE	SP	LP			C	VB	VE	SP	LP	
Atlas[1]	8	1	0	0	0			6	2	0	0	0			3	0	0	0	0			3	2	0	0	0			0	0	0	0	0			0	0	0	0	0	
Atlas[2]	0	0	0	0	0			0	2	0	0	0			0	6	4	0	0			0	4	0	0	0			0	1	4	0	10			0	6	4	0	2	
Axis[1]	8	1	0	0	0			5	0	0	0	0			3	0	0	0	0			2	2	0	1	0			0	0	0	0	0			0	0	0	0	0	
Axis[2]	0	0	0	0	0			0	1	0	0	0			0	7	0	0	0			0	5	0	1	0			0	8	1	3	0			0	9	2	4	0	
Cervical[1]	24	8	0	1	0			5	4	0	0	0			8	2	0	0	0			1	7	1	0	0			0	0	0	0	0			0	0	0	0	0	
Cervical[2]	0	2	2	1	0			0	15	0	2	0			0	43	0	0	0			0	35	4	5	3			0	27	5	4	0			2	11	4	17	0	
Thorasic[1]	36	33	8	31	0			11	25	0	2	0			16	7	2	2	0			4	17	0	0	0			0	0	0	0	0			0	0	0	0	0	
Thorasic[2]	0	3	1	2	0			0	27	2	4	0			0	90	3	5	0			0	93	13	11	9			0	24	7	14	3			6	22	21	11	6	
Lumbar[1]	11	51	6	0	0			10	17	0	0	0			31	20	3	0	0			7	19	2	1	1			0	0	0	0	0			0	0	0	0	0	
Lumbar[2]	0	0	0	0	0			0	23	0	0	0			0	22	1	1	5			0	28	12	0	6			0	9	21	8	13			4	37	22	5	18	
Sacrum[1]	24	16	0	0	0			15	2	0	0	0			28	9	0	0	0			9	0	0	0	0			0	0	0	0	0			0	0	0	0	0	
Sacrum[2]	0	0	0	0	0			0	1	0	0	0			0	0	0	0	0			0	10	0	0	0			0	11	6	1	4			0	13	0	0	0	
	Undigested[1]																																								
	Digested[2]																																								

APPENDIX E

Bone surface modification frequencies, totals, and anatomical locations for the bald eagle modified samples.

Eagle	Rabbit																									
	Punctures Total	Un-digested Punctures	Digested Punctures	**Pits Total**	Un-digested Pits	Digested Pits	**Crenulated edge Total**	Un-digested Crenulated edge	Digested Crenulated edge	**Fracture edge Total**	Un-digested Fractured edge	Digested Fractured edge	**Notch Total**	Un-digested Notch	Digested Notch	**Scores Total**	Un-digested Scores	Digested Scores	**Digested Total**	Un-digested Digested	Digested Digested	**Total Surface Mods**
Cran (Max)	**2 (5.0)**	1 (2.9)	1 (20.0)	**1 (2.5)**	1 (2.9)	0 (0.0)	**15 (37.5)**	14 (40.0)	1 (20.0)	**14 (35.0)**	14 (40.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.5)**	1 (2.9)	0 (0.0)	**5 (12.5)**	0 (0.0)	5 (100)	**38 (95.0)**
Man	**2 (6.5)**	2 (7.4)	0 (0.0)	**1 (3.2)**	1 (3.7)	0 (0.0)	**4 (12.9)**	4 (14.8)	0 (0.0)	**14 (45.2)**	13 (48.1)	1 (25.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (6.5)**	2 (7.4)	0 (0.0)	**4 (12.9)**	0 (0.0)	4 (100)	**27 (87.1)**
Incisors in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Upper cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Lower cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (5.3)**	0 (0.0)	5 (100)	**5 (5.3)**
Incisors isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (100)**	0 (0.0)	4 (100)	**4 (100)**
Upper cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Lower cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (100)**	0 (0.0)	3 (100)	**3 (100)**
Atlas	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Axis	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Cerv	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**10 (26.3)**	10 (30.3)	0 (0.0)	**2 (5.3)**	2 (6.1)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (13.2)**	0 (0.0)	5 (100)	**17 (44.7)**
Thor	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**35 (30.7)**	33 (30.6)	2 (33.3)	**35 (30.7)**	33 (30.6)	2 (33.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**6 (4.3)**	0 (0.0)	6 (100)	**76 (66.7)**
Lum	**1 (1.5)**	1 (1.5)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**27 (39.7)**	27 (39.7)	0 (0.0)	**27 (39.7)**	27 (39.7)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**55 (80.9)**
Sac	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**15 (37.5)**	15 (37.5)	0 (0.0)	**3 (7.5)**	3 (7.5)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**18 (45.0)**
Caudal	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**22 (21.2)**	0 (0.0)	22 (100)	**22 (21.2)**
Rib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**123 (56.4)**	119 (62.3)	4 (14.8)	**53 (24.3)**	48 (25.1)	5 (18.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (0.5)**	1 (0.5)	0 (0.0)	**27 (12.4)**	0 (0.0)	27 (100)	**204 (93.6)**
Stern	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (15.4)**	0 (0.0)	4 (100)	**4 (15.4)**
Scap	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (28.9)**	10 (33.3)	1 (12.5)	**18 (47.4)**	18 (60.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.6)**	1 (3.3)	0 (0.0)	**8 (21.1)**	0 (0.0)	8 (100)	**38 (100)**
Hum	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (6.3)**	2 (7.4)	0 (0.0)	**2 (6.3)**	2 (7.4)	0 (0.0)	**13 (40.6)**	13 (48.1)	0 (0.0)	**1 (3.1)**	1 (3.7)	0 (0.0)	**6 (18.8**	6 (22.2)	0 (0.0)	**5 (15.6)**	0 (0.0)	5 (100)	**29 (90.6)**
Rad	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (22.7)**	0 (0.0)	5 (100)	**5 (22.7)**
Uln	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (9.1)**	2 (11.1)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (4.5)**	1 (5.6)	0 (0.0)	**4 (18.2)**	0 (0.0)	4 (100)	**7 (31.8)**
Mtc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (11.8)**	0 (0.0)	12 (100)	**12 (11.8)**
Pel	**1 (4.8)**	1 (5.0)	0 (0.0)	**2 (9.5)**	2 (10.0)	0 (0.0)	**16 (76.2)**	16 (80.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (4.8)**	1 (5.0)	0 (0.0)	**1 (4.8)**	0 (0.0)	1 (100)	**21 (100)**
Fem	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Pat	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Tib	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (4.3)**	1 (4.3)	0 (0.0)	**3 (13.0)**	3 (13.1)	0 (0.0)	**3 (13.0)**	3 (13.0)	0 (0.0)	**1 (4.3)**	1 (4.3)	0 (0.0)	**2 (8.7)**	2 (8.7)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**10 (43.5)**
Fib	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**
Calc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Ast	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Mtt	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Carp/tars	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (4.7)**	0 (0.0)	11 (100)	**11 (4.7)**
Phlx 1/2	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**18 (5.3)**	0 (0.0)	18 (100)	**21 (6.2)**
Phlx 3	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (2.9)**	0 (0.0)	5 (100)	**5 (2.9)**
NISP Total	**6 (0.3)**	5 (0.3)	1 (0.6)	**7 (0.3)**	7 (0.4)	0 (0.0)	**261 (12.2)**	253 (12.8)	8 (5.2)	**184 (8.6)**	176 (8.9)	8 (5.2)	**2 (0.1)**	2 (0.1)	0 (0.0)	**15 (0.7**	15 (0.8)	0 (0.0)	**154 (7.2)**	0 (0.0)	154 (100)	**632 (29.6)**
Vert indet	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**69 (100)**	0 (0.0)	69 (100)	**69 (100)**
LBS	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
FRG>2mm	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**54 (100)**	0 (0.0)	54 (100)	**54 (100)**
Tooth frag	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (100)**	0 (0.0)	3 (100)	**3 (100)**
N Total	**6 (0.3)**	5 (0.3)	1 (0.4)	**7 (0.3)**	7 (0.4)	0 (0.0)	**261 (11.5)**	253 (12.8)	8 (2.9)	**184 (8.1)**	176 (8.9)	8 (2.9)	**2 (0.1)**	2 (0.1)	0 (0.0)	**15 (0.7**	15 (0.8)	0 (0.0)	**280 (12.4**	0 (0.0)	280 (100)	**755 (33.4)**

Eagle	Guinea Pig																					
	Punc-tures Total	Un-digested Punctures	Digested Punctures	**Pits Total**	Un-digested Pits	Digested Pits	**Cren-ulated edge Total**	Un-digested Cren-ulated edge	Digested Cren-ulated edge	**Fracture d edge Total**	Un-digested Frac-tured edge	Digested Frac-tured edge	**Notch Total**	Un-digested Notch	Digested Notch	**Scores Total**	Un-digested Scores	Digested Scores	**Digested Total**	Un-digested Digested	Digested Digested	**Total Surface Mods**
Cran (Max)	**3 (9.4)**	2 (13.3)	1 (5.9)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (12.5)**	4 (26.7)	0 (0.0)	**9 (28.1)**	9 (60.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**17 (53.1)**	0 (0.0)	17 (100)	**33 (103)**
Man	**1 (4.2)**	1 (10.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (12.5)**	3 (30.0)	0 (0.0)	**4 (16.7)**	4 (40.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**14 (58.3)**	0 (0.0)	14 (100)	**22 (91.7)**
Incisors in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (8.3)**	0 (0.0)	2 (100)	**2 (8.3)**
Upper cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (13.5)**	0 (0.0)	5 (100)	**5 (13.5)**
Lower cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**7 (14.9)**	0 (0.0)	7 (100)	**7 (14.9)**
Incisors isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**14 (100)**	0 (0.0)	14 (100)	**14 (100)**
Upper cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**24 (100)**	0 (0.0)	24 (100)	**24 (100)**
Lower cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**17 (100)**	0 (0.0)	17 (100)	**17 (100)**
Atlas	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (10.0)**	1 (12.5)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (20.0)**	0 (0.0)	2 (100)	**3 (30.0)**
Axis	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (16.7)**	0 (0.0)	1 (100)	**1 (16.7)**
Cerv	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**6 (23.1)**	6 (66.7)	0 (0.0)	**1 (3.8)**	1 (11.1)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**17 (65.4)**	0 (0.0)	17 (100)	**24 (92.3)**
Thor	**2 (2.8)**	2 (5.3)	0 (0.0)	**1 (1.4)**	1 (2.6)	0 (0.0)	**15 (21.1)**	15 (39.5)	0 (0.0)	**11 (15.5)**	9 (23.7)	2 (6.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**33 (46.5)**	0 (0.0)	33 (100)	**62 (87.3)**
Lum	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**9 (18.0)**	8 (29.6)	1 (4.3)	**6 (12.0)**	5 (18.5)	1 (4.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**23 (46.0)**	0 (0.0)	23 (100)	**38 (76.0)**
Sac	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (5.6)**	1 (5.9)	0 (0.0)	**1 (5.6)**	1 (5.9)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (5.6)**	0 (0.0)	1 (100)	**3 (16.7)**
Caudal	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**15 (75.0)**	0 (0.0)	15 (100)	**15 (75.0)**
Rib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**46 (38.3)**	43 (69.4)	3 (5.2)	**15 (12.5)**	14 (22.6)	1 (1.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**58 (48.3)**	0 (0.0)	58 (100)	**119 (99.2)**
Stern	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (100)**	1 (100)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (100)**
Scap	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**10 (33.3)**	9 (47.4)	1 (9.1)	**9 (30.0)**	9 (47.4)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (36.7)**	0 (0.0)	11 (100)	**30 (100)**
Hum	**1 (4.3)**	0 (0.0)	1 (9.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (4.3)**	1 (8.3)	0 (0.0)	**2 (8.7)**	2 (16.7)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (47.8)**	0 (0.0)	11 (100)	**15 (65.2)**
Rad	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (16.7)**	4 (30.8)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (45.8)**	0 (0.0)	11 (100)	**15 (62.5)**
Uln	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (16.7)**	4 (30.8)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (45.8)**	0 (0.0)	11 (100)	**15 (62.5)**
Mtc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**37 (43.5)**	0 (0.0)	37 (100)	**37 (43.5)**
Pel	**4 (14.3**	4 (19.0)	0 (0.0)	**3 (10.7**	3 (14.3)	0 (0.0)	**15 (53.6)**	15 (71.4)	0 (0.0)	**3 (10.7)**	3 (14.3)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (10.7**	3 (14.3)	0 (0.0)	**7 (25.0)**	0 (0.0)	7 (100)	**35 (125)**
Fem	**2 (7.1)**	2 (10.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (10.7)**	3 (15.0)	0 (0.0)	**6 (21.4)**	6 (30.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.6)**	1 (5.0)	0 (0.0)	**8 (28.6)**	0 (0.0)	8 (100)	**20 (71.4)**
Pat	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Tib	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.1)**	1 (4.8)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**10 (31.3)**	10 (47.6)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.1)**	1 (4.8)	0 (0.0)	**11 (34.4)**	0 (0.0)	11 (100)	**23 (71.9)**
Fib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**10 (47.6)**	10 (47.6)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Calc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (10.0)**	0 (0.0)	2 (100)	**2 (10.0)**
Ast	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (5.3)**	0 (0.0)	1 (100)	**1 (5.3)**
Mtt	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**7 (11.5)**	0 (0.0)	7 (100)	**7 (11.5)**
Carp/tars	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**27 (17.6)**	0 (0.0)	27 (100)	**27 (17.6)**
Phlx 1/2	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**68 (27.0)**	0 (0.0)	68 (100)	**68 (27.0)**
Phlx 3	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**21 (18.6)**	0 (0.0)	21 (100)	**21 (18.6)**
NISP Total	**13 (0.9**	11 (1.1)	2 (0.4)	**5 (0.3)**	5 (0.5)	0 (0.0)	**115 (7.8)**	110 (11.1)	5 (1.0)	**95 (6.5)**	91 (9.2)	4 (0.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (0.3)**	5 (0.5)	0 (0.0)	**483 (32.9**	0 (0.0)	483 (100)	**643 (43.7)**
Vert indet	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**43 (100)**	0 (0.0)	43 (100)	**43 (100)**
LBS	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**9 (100)**	0 (0.0)	9 (100)	**9 (100)**
FRG>2mm	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**128 (100)**	0 (0.0)	128 (100)	**128 (100)**
Tooth frag	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**52 (100)**	0 (0.0)	52 (100)	**52 (100)**
N Total	**13 (0.8**	11 (1.1)	2 (0.3)	**5 (0.3)**	5 (0.5)	0 (0.0)	**115 (6.8)**	110 (11.1)	5 (0.7)	**95 (5.6)**	91 (9.2)	4 (0.6)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (0.3)**	5 (0.5)	0 (0.0)	**715 (42.0**	0 (0.0)	715 (100)	**948 (55.7)**

APPENDIX F

Bone surface modification frequencies, totals, and anatomical locations for the great horned owl modified samples.

Owl	Rabbit																									
	Punctures Total	Undigested Punctures	Digested Punctures	Pits Total	Undigested Pits	Digested Pits	Crenulated edge Total	Undigested Crenulated edge	Digested Crenulated edge	Fracture Total	Undigested Fractured edge	Digested Fractured edge	Notch Total	Undigested Notch	Digested Notch	Scores Total	Undigested Scores	Digested Scores	Digested Total	Undigested Digested	Digested Digested	Total Surface Mods
Cran (Max)	**4 (3.8)**	0 (0.0)	4 (5.0)	**3 (2.9)**	2 (8.3)	1 (1.3)	**11 (10.6)**	5 (20.8)	6 (7.5)	**8 (7.7)**	3 (12.5)	5 (6.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**80 (76.9)**	0 (0.0)	80 (100)	**106 (102)**
Man	**1 (1.7)**	0 (0.0)	1 (2.2)	**4 (6.9)**	2 (16.7)	2 (4.3)	**3 (5.2)**	1 (8.3)	2 (4.3)	**8 (13.8)**	2 (16.7)	6 (13.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.7)**	0 (0.0)	1 (2.2)	**46 (79.3)**	0 (0.0)	46 (100)	**63 (109)**
Incisors in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**7 (20.0)**	0 (0.0)	7 (100)	**7 (20.0)**
Upper cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**8 (14.3)**	0 (0.0)	8 (100)	**8 (14.3)**
Lower cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**21 (34.4)**	0 (0.0)	21 (100)	**21 (34.4)**
Incisors isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**18 (100)**	0 (0.0)	18 (100)	**18 (100)**
Upper cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**71 (100)**	0 (0.0)	71 (100)	**71 (100)**
Lower cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**37 (100)**	0 (0.0)	37 (100)	**37 (100)**
Atlas	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**10 (76.9)**	0 (0.0)	10 (100)	**10 (76.9)**
Axis	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**7 (70.0)**	0 (0.0)	7 (100)	**7 (70.0)**
Cerv	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (3.8)**	0 (0.0)	2 (4.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**43 (81.1)**	0 (0.0)	43 (100)	**45 (84.9)**
Thor	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (2.4)**	2 (7.4)	1 (1.0)	**7 (5.6)**	1 (3.7)	6 (6.1)	**5 (4.0)**	0 (0.0)	5 (5.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**98 (78.4)**	0 (0.0)	98 (100)	**113 (90.4)**
Lum	**4 (4.8)**	3 (5.6)	1 (3.4)	**3 (3.6)**	3 (5.6)	0 (0.0)	**19 (22.9)**	10 (18.5)	9 (31.0)	**12 (14.5)**	3 (5.6)	9 (31.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.2)**	1 (1.9)	0 (0.0)	**29 (34.9)**	0 (0.0)	29 (100)	**68 (81.9)**
Sac	**2 (5.4)**	2 (5.4)	0 (0.0)	**3 (8.1)**	3 (8.1)	0 (0.0)	**9 (24.3)**	9 (24.3)	0 (0.0)	**1 (2.7)**	1 (2.7)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**15 (40.5)**
Caudal	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**45 (34.6)**	0 (0.0)	45 (100)	**45 (34.6)**
Rib	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (0.2)**	0 (0.0)	1 (0.2)	**26 (4.6)**	3 (4.6)	23 (4.6)	**43 (7.6)**	10 (15.4)	33 (6.6)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**501 (88.5**	0 (0.0)	501 (100)	**571 (100)**
Stern	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**15 (100)**	0 (0.0)	15 (100)	**15 (100)**
Scap	**1 (0.9)**	0 (0.0)	1 (1.1)	**6 (5.4)**	4 (16.7)	2 (2.3)	**9 (8.0)**	2 (8.3)	7 (8.0)	**4 (3.6)**	2 (8.3)	2 (2.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (0.9)**	1 (4.2)	0 (0.0)	**88 (78.6)**	0 (0.0)	88 (100)	**109 (97.3)**
Hum	**3 (10.3**	1 (6.7)	2 (14.3)	**4 (13.8**	4 (26.7)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (13.8)**	2 (13.3)	2 (14.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.4)**	1 (6.7)	0 (0.0)	**14 (48.3)**	0 (0.0)	14 (100)	**26 (89.7)**
Rad	**1 (3.8)**	0 (0.0)	1 (8.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (7.7)**	1 (7.1)	1 (8.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (46.2)**	0 (0.0)	12 (100)	**15 (57.7)**
Uln	**1 (3.8)**	0 (0.0)	1 (8.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (7.7)**	2 (14.3)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (46.2)**	0 (0.0)	12 (100)	**15 (57.7)**
Mtc	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (1.8)**	1 (1.5)	1 (2.2)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**45 (40.9)**	0 (0.0)	45 (100)	**47 (42.7)**
Pel	**6 (23.1**	5 (20.0)	1 (100)	**6 (23.1**	6 (24.0)	0 (0.0)	**19 (73.1)**	19 (76.0)	0 (0.0)	**2 (7.7)**	2 (8.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.8)**	1 (4.0)	0 (0.0)	**1 (3.8)**	0 (0.0)	1 (100)	**35 (135)**
Fem	**2 (6.9)**	1 (4.3)	1 (16.7)	**4 (13.8**	3 (13.0)	1 (16.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**6 (20.7)**	4 (17.4)	2 (33.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**6 (20.7)**	0 (0.0)	6 (100)	**18 (62.1)**
Pat	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**
Tib	**2 (8.7)**	1 (5.6)	1 (20.0)	**6 (26.1**	5 (27.8)	1 (20.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (21.7)**	0 (0.0)	5 (100)	**13 (56.5)**
Fib	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**
Calc	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (5.0)**	0 (0.0)	1 (20.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (25.0)**	0 (0.0)	5 (100)	**6 (30.0)**
Ast	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (25.0)**	0 (0.0)	5 (100)	**5 (25.0)**
Mtt	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.2)**	1 (1.6)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**20 (23.8)**	0 (0.0)	20 (100)	**21 (25.5)**
Carp/tars	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**49 (23.2)**	0 (0.0)	49 (100)	**49 (23.2)**
Phlx 1/2	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**98 (28.6)**	0 (0.0)	98 (100)	**21 (6.1)**
Phlx 3	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**48 (26.5)**	0 (0.0)	48 (100)	**5 (2.8)**
NISP Total	**27 (1.0**	13 (1.0)	14 (1.0)	**47 (1.7**	36 (2.8)	11 (0.8)	**103 (3.8)**	50 (3.9)	53 (3.7)	**99 (3.6)**	32 (2.5)	67 (4.6)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (0.2)**	4 (0.3)	1 (0.1)	**1444 (52.**	0 (0.0)	1444 (100	**1605 (58.8**
Vert indet	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**45 (100)**	0 (0.0)	45 (100)	**45 (100)**
LBS	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**22 (100)**	0 (0.0)	22 (100)	**22 (100)**
FRGs2mm	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**309 (100)**	0 (0.0)	309 (100)	**309 (100)**
Tooth frag	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**79 (100)**	0 (0.0)	79 (100)	**0 (0.0)**
N Total	**27 (0.8**	13 (1.0)	14 (0.7)	**47 (1.5**	36 (2.8)	11 (0.6)	**103 (3.2)**	50 (3.9)	53 (2.8)	**99 (3.1)**	32 (2.5)	67 (3.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (0.2)**	4 (0.3)	1 (0.1)	**1899 (59.**	0 (0.0)	1899 (100)	

Owl	Guinea Pig																					
	Punc-tures Total	Un-digested Punc-tures	Digested Punc-tures	**Pits Total**	Un-digested Pits	Digested Pits	**Cren-ulated edge Total**	Un-digested Cren-ulated edge	Digested Cren-ulated edge	**Fracture d edge Total**	Un-digested Frac-tured edge	Digested Frac-tured edge	**Notch Total**	Un-digested Notch	Digested Notch	**Scores Total**	Un-digested Scores	Digested Scores	**Digested Total**	Un-digested Digested	Digested Digested	**Total Surface Mods**
Cran (Max)	**1 (1.7)**	1 (4.2)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**9 (15.0)**	7 (29.2)	2 (5.6)	**11 (18.3)**	8 (33.3)	3 (8.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**36 (60.0)**	0 (0.0)	36 (100)	**57 (95.0)**
Man	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.0)**	1 (6.3)	0 (0.0)	**6 (18.2)**	6 (37.5)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.0)**	1 (6.3)	0 (0.0)	**17 (51.5)**	0 (0.0)	17 (100)	**25 (75.8)**
Incisors in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (16.1)**	0 (0.0)	5 (100)	**5 (16.1)**
Upper cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (20.7)**	0 (0.0)	12 (100)	**12 (20.7)**
Lower cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**38 (48.7)**	0 (0.0)	38 (100)	**38 (48.7)**
Incisors isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (100)**	0 (0.0)	11 (100)	**11 (100)**
Upper cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**19 (86.4)**	0 (0.0)	19 (100)	**19 (86.4)**
Lower cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (100)**	0 (0.0)	1 (100)	**1 (100)**
Atlas	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (11.1)**	1 (20.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (44.4)**	0 (0.0)	4 (100)	**5 (55.6)**
Axis	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (27.3)**	3 (60.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**6 (54.5)**	0 (0.0)	6 (100)	**9 (81.8)**
Cerv	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.8)**	1 (11.1)	0 (0.0)	**4 (7.1)**	4 (44.4)	0 (0.0)	**4 (7.1)**	0 (0.0)	4 (8.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**47 (83.9)**	0 (0.0)	47 (100)	**56 (100)**
Thor	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (8.2)**	9 (42.9)	3 (2.4)	**8 (5.4)**	3 (14.3)	5 (4.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**126 (85.7**	0 (0.0)	126 (100)	**146 (99.3)**
Lum	**2 (2.6)**	1 (3.3)	1 (2.2)	**0 (0.0)**	0 (0.0)	0 (0.0)	**18 (23.7)**	13 (43.3)	5 (10.9)	**5 (6.6)**	2 (6.7)	3 (6.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**46 (60.5)**	0 (0.0)	46 (100)	**71 (93.4)**
Sac	**1 (5.3)**	0 (0.0)	1 (10.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (5.3)**	1 (11.1)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**10 (52.6)**	0 (0.0)	10 (100)	**12 (63.2)**
Caudal	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (33.3)**	0 (0.0)	12 (100)	**12 (33.3)**
Rib	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (0.3)**	1 (1.6)	0 (0.0)	**48 (12.7)**	37 (60.7)	11 (3.5)	**11 (2.9)**	11 (18.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**318 (83.9**	0 (0.0)	318 (100)	**378 (99.7)**
Stern	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (6.3)**	0 (0.0)	1 (6.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**16 (100)**	0 (0.0)	16 (100)	**17 (106)**
Scap	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.6)**	1 (7.7)	0 (0.0)	**13 (20.3)**	12 (92.3)	1 (2.0)	**2 (3.1)**	1 (7.7)	1 (2.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**51 (79.7)**	0 (0.0)	51 (100)	**67 (105)**
Hum	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.3)**	0 (0.0)	1 (4.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**7 (23.3)**	1 (14.3)	6 (26.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**23 (76.7)**	0 (0.0)	23 (100)	**31 (103)**
Rad	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (10.3)**	0 (0.0)	3 (13.6)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**22 (75.9)**	0 (0.0)	22 (100)	**25 (86.2)**
Uln	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (15.4)**	1 (14.3)	3 (15.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**19 (73.1)**	0 (0.0)	19 (100)	**23 (88.5)**
Mtc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**55 (66.3)**	0 (0.0)	55 (100)	**55 (66.3)**
Pel	**4 (16.0**	2 (10.5)	2 (33.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (48.0)**	12 (63.2)	0 (0.0)	**4 (16.0)**	4 (21.1)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (8.0)**	2 (10.5)	0 (0.0)	**6 (24.0)**	0 (0.0)	6 (100)	**28 (112)**
Fem	**1 (2.9)**	0 (0.0)	1 (7.7)	**1 (2.9)**	1 (4.8)	0 (0.0)	**2 (5.9)**	1 (4.8)	1 (7.7)	**12 (35.3)**	10 (47.6)	2 (15.4)	**1 (2.9)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**13 (38.2)**	0 (0.0)	13 (100)	**30 (88.2)**
Pat	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**7 (41.2)**	0 (0.0)	7 (100)	**7 (41.2)**
Tib	**1 (3.1)**	0 (0.0)	1 (5.0)	**2 (6.3)**	1 (8.3)	1 (5.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.1)**	1 (8.3)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**20 (62.5)**	0 (0.0)	20 (100)	**24 (75.0)**
Fib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (10.5)**	1 (9.1)	1 (12.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**8 (42.1)**	0 (0.0)	8 (100)	**10 (52.6)**
Calc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**8 (40.0)**	0 (0.0)	8 (100)	**8 (40.0)**
Ast	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**8 (40.0)**	0 (0.0)	8 (100)	**8 (40.0)**
Mtt	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**28 (43.8)**	0 (0.0)	28 (100)	**28 (43.8)**
Carp/tars	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**71 (46.7)**	0 (0.0)	71 (100)	**71 (46.7)**
Phlx 1/2	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**147 (53.5**	0 (0.0)	147 (100)	**21 (7.6)**
Phlx 3	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**64 (50.0)**	0 (0.0)	64 (100)	**5 (3.9)**
NISP Total	**10 (0.5**	4 (0.5)	6 (0.5)	**8 (0.4)**	5 (0.6)	3 (0.2)	**124 (6.0)**	101 (12.8)	23 (1.8)	**80 (3.9)**	49 (6.2)	31 (2.4)	**1 (0.1)**	0 (0.0)	0 (0.0)	**3 (0.1)**	3 (0.4)	0 (0.0)	**1274 (61.**	0 (0.0)	1274 (100	**1305 (63.3**
Vert indet	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**65 (100)**	0 (0.0)	66 (100)	**66 (101)**
LBS	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (3.4)**	0 (0.0)	1 (3.4)	**0 (0.0)**	0 (0.0)	0 (0.0)	**29 (100)**	0 (0.0)	29 (100)	**30 (103)**
FRG>2mm	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**485 (100)**	0 (0.0)	485 (100)	**485 (100)**
Tooth frag	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**44 (100)**	0 (0.0)	44 (100)	**44 (100)**
N Total	**10 (0.4**	4 (0.5)	6 (0.3)	**8 (0.3)**	5 (0.6)	3 (0.2)	**124 (4.6)**	101 (12.8)	23 (1.2)	**80 (3.0)**	49 (6.2)	31 (1.6)	**2 (0.1)**	0 (0.0)	1 (0.1)	**3 (0.1)**	3 (0.4)	0 (0.0)	**1898 (70.**	0 (0.0)	1898 (100	**2114 (78.8**

APPENDIX G

Bone surface modification frequencies, totals, and anatomical locations for the coyote modified samples.

Coyote	Rabbit																															
	Punctures Total	Un-digested Punctures	Digested Punctures	Pits Total	Un-digested Pits	Digested Pits	Crenulated edge Total	Un-digested Crenulated edge	Digested Crenulated edge	Fracture Total	Un-digested Fractured edge	Digested Fractured edge	Notch Total	Un-digested Notch	Digested Notch	Scores Total	Un-digested Scores	Digested Scores	Digested Total	Un-digested Digested	Digested Digested	Total Surface Mods
Cran (Max)	**3 (2.0)**	0 (0.0)	3 (2.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**7 (4.6)**	5 (41.7)	2 (1.4)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**140 (92.1**	0 (0.0)	140 (100)	**150 (98.7)**
Man	**2 (2.1)**	0 (0.0)	2 (2.2)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (2.1)**	0 (0.0)	2 (2.2)	**5 (5.2)**	4 (100)	1 (1.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (2.1)**	0 (0.0)	2 (2.2)	**93 (95.9)**	0 (0.0)	93 (100)	**104 (107)**
Incisors in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**17 (89.5)**	0 (0.0)	17 (100)	**17 (89.5)**
Upper cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**30 (71.4)**	0 (0.0)	30 (100)	**30 (71.4)**
Lower cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**33 (73.3)**	0 (0.0)	33 (100)	**33 (73.3)**
Incisors isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**31 (100)**	0 (0.0)	31 (100)	**31 (100)**
Upper cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**78 (100)**	0 (0.0)	78 (100)	**78 (100)**
Lower cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**55 (100)**	0 (0.0)	55 (100)	**55 (100)**
Atlas	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (6.7)**	0 (0.0)	1 (6.7)	**3 (20.0)**	0 (0.0)	3 (20.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**15 (100)**	0 (0.0)	15 (100)	**19 (127)**
Axis	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (8.3)**	0 (0.0)	1 (8.3)	**2 (16.7)**	0 (0.0)	2 (16.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (100)**	0 (0.0)	12 (100)	**15 (125)**
Cerv	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (5.6)**	0 (0.0)	2 (5.6)	**4 (11.1)**	0 (0.0)	4 (11.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**36 (100)**	0 (0.0)	36 (100)	**42 (117)**
Thor	**1 (2.1)**	0 (0.0)	1 (2.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (4.2)**	0 (0.0)	2 (4.2)	**7 (14.6)**	0 (0.0)	7 (14.6)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**48 (100)**	0 (0.0)	48 (100)	**58 (121)**
Lum	**4 (7.8)**	0 (0.0)	4 (7.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.0)**	0 (0.0)	1 (2.0)	**8 (15.7)**	0 (0.0)	8 (15.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.0)**	0 (0.0)	1 (2.0)	**51 (100)**	0 (0.0)	51 (100)	**65 (128)**
Sac	**1 (4.5)**	0 (0.0)	1 (4.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**3 (13.6)**	0 (0.0)	3 (13.6)	**7 (31.8)**	0 (0.0)	7 (31.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (4.5)**	0 (0.0)	1 (4.5)	**22 (100)**	0 (0.0)	22 (100)	**34 (155)**
Caudal	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.3)**	0 (0.0)	1 (1.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**65 (85.5)**	0 (0.0)	65 (100)	**66 (86.8)**
Rib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**6 (2.0)**	0 (0.0)	6 (2.0)	**35 (11.7)**	0 (0.0)	35 (11.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**298 (99.7**	0 (0.0)	298 (100)	**339 (113)**
Stern	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**14 (100)**	0 (0.0)	14 (100)	**14 (100)**
Scap	**1 (3.6)**	0 (0.0)	1 (3.6)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (7.1)**	0 (0.0)	2 (7.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**28 (100)**	0 (0.0)	28 (100)	**31 (111)**
Hum	**2 (2.5)**	0 (0.0)	2 (2.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**9 (11.4)**	0 (0.0)	9 (11.4)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.3)**	0 (0.0)	1 (1.3)	**79 (100)**	0 (0.0)	79 (100)	**91 (115)**
Rad	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (5.0)**	0 (0.0)	2 (5.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**38 (95.0)**	0 (0.0)	38 (100)	**40 (100)**
Uln	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (5.7)**	0 (0.0)	2 (6.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.9)**	0 (0.0)	1 (3.0)	**33 (94.3)**	0 (0.0)	33 (100)	**36 (103)**
Mtc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**9 (7.9)**	0 (0.0)	9 (10.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**89 (78.1)**	0 (0.0)	89 (100)	**98 (86.0)**
Pel	**3 (4.5)**	0 (0.0)	3 (4.5)	**2 (3.0)**	0 (0.0)	2 (3.0)	**1 (1.5)**	0 (0.0)	1 (1.5)	**6 (9.0)**	0 (0.0)	6 (9.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**67 (100)**	0 (0.0)	67 (100)	**79 (118)**
Fem	**1 (1.6)**	0 (0.0)	1 (1.6)	**1 (1.6)**	0 (0.0)	1 (1.6)	**1 (1.6)**	0 (0.0)	1 (1.6)	**12 (19.0)**	0 (0.0)	12 (19.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.6)**	0 (0.0)	1 (1.6)	**63 (100)**	0 (0.0)	63 (100)	**79 (125)**
Pat	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**20 (100)**	0 (0.0)	20 (100)	**20 (100)**
Tib	**2 (2.7)**	0 (0.0)	2 (3.3)	**1 (1.4)**	0 (0.0)	1 (1.6)	**1 (1.4)**	0 (0.0)	1 (8.3)	**10 (13.7)**	0 (0.0)	10	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.4)**	0 (0.0)	1 (1.6)	**61 (83.6)**	0 (0.0)	61 (100)	**76 (104)**
Fib	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**	n/a	n/a	**n/a**
Calc	**1 (4.5)**	0 (0.0)	1 (6.3)	**2 (9.1)**	0 (0.0)	2 (12.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**16 (72.7)**	0 (0.0)	16 (100)	**19 (86.4)**
Ast	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (10.0**	0 (0.0)	2 (14.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**14 (70.0)**	0 (0.0)	14 (100)	**16 (80.0)**
Mtt	**1 (0.9)**	1 (4.2)	0 (0.0)	**1 (0.9)**	0 (0.0)	1 (1.2)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (10.1)**	0 (0.0)	11 (12.9)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**85 (78.0)**	0 (0.0)	85 (100)	**98 (89.9)**
Carp/tars	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**99 (61.1)**	0 (0.0)	99 (100)	**99 (61.1)**
Phlx 1/2	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**5 (1.3)**	0 (0.0)	5 (1.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**293 (75.9**	0 (0.0)	293 (100)	**21 (5.4)**
Phlx 3	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (1.3)**	0 (0.0)	2 (1.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**115 (71.9**	0 (0.0)	115 (100)	**5 (3.1)**
NISP Total	**22 (0.9**	1 (0.3)	21 (1.0)	**9 (0.4)**	0 (0.0)	9 (0.4)	**21 (0.9)**	1 (0.3)	20 (0.9)	**149 (6.0)**	9 (2.7)	140 (6.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**8 (0.3)**	0 (0.0)	8 (0.4)	**2138 (86.**	0 (0.0)	2138 (100	**1958 (79.3**
Vert indet	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**125 (100**	0 (0.0)	125 (100)	**125 (100)**
LBS	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**156 (100**	0 (0.0)	156 (100)	**156 (100)**
FRG>2mm	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1111 (100**	0 (0.0)	1111 (100	**1111 (100)**
Tooth frag	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**41 (100)**	0 (0.0)	41 (100)	**41 (100)**
N Total	**22 (0.6**	1 (0.3)	21 (0.6)	**9 (0.2)**	0 (0.0)	9 (0.3)	**21 (0.5)**	1 (0.3)	20 (0.6)	**149 (3.8)**	9 (2.7)	140 (3.9)	**0 (0.0)**	0 (0.0)	0 (0.0)	**8 (0.2)**	0 (0.0)	8 (0.2)	**3571 (91**	0 (0.0)	3571 (100	**3780 (96.8**

Coyote	Guinea Pig																					
	Punc-tures Total	Un-digested Punc-tures	Digested Punc-tures	**Pits Total**	Un-digested Pits	Digested Pits	**Cren-ulated edge Total**	Un-digested Cren-ulated edge	Digested Cren-ulated edge	**Fracture d edge Total**	Un-digested Frac-tured edge	Digested Frac-tured edge	**Notch Total**	Un-digested Notch	Digested Notch	**Scores Total**	Un-digested Scores	Digested Scores	**Digested Total**	Un-digested Digested	Digested Digested	**Total Surface Mods**
Cran (Max)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.1)**	0 (0.0)	1 (1.1)	**2 (2.2)**	0 (0.0)	2 (2.2)	**5 (0.0)**	0 (0.0)	5 (5.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**91 (100)**	0 (0.0)	91 (100)	**99 (109)**
Man	**1 (1.6)**	0 (0.0)	1 (1.6)	**1 (1.6)**	0 (0.0)	1 (1.6)	**1 (1.6)**	0 (0.0)	1 (1.6)	**3 (0.0)**	0 (0.0)	3 (4.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**64 (100)**	0 (0.0)	64 (100)	**70 (109)**
Incisors in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**24 (100)**	0 (0.0)	24 (100)	**24 (100)**
Upper cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**33 (100)**	0 (0.0)	33 (100)	**33 (100)**
Lower cheek in situ	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**58 (100)**	0 (0.0)	58 (100)	**58 (100)**
Incisors isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**22 (100)**	0 (0.0)	22 (100)	**22 (100)**
Upper cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (100)**	0 (0.0)	11 (100)	**11 (100)**
Lower cheek isolated	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**6 (100)**	0 (0.0)	6 (100)	**6 (100)**
Atlas	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (8.3)**	0 (0.0)	1 (8.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**12 (100)**	0 (0.0)	12 (100)	**13 (108)**
Axis	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**15 (100)**	0 (0.0)	15 (100)	**15 (100)**
Cerv	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**34 (100)**	0 (0.0)	34 (100)	**34 (100)**
Thor	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**66 (100)**	0 (0.0)	66 (100)	**66 (100)**
Lum	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.2)**	0 (0.0)	1 (1.2)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**86 (100)**	0 (0.0)	86 (100)	**87 (101)**
Sac	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**13 (100)**	0 (0.0)	13 (100)	**13 (100)**
Caudal	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**37 (100)**	0 (0.0)	37 (100)	**37 (100)**
Rib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**97 (100)**	0 (0.0)	97 (100)	**97 (100)**
Stern	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**26 (100)**	0 (0.0)	26 (100)	**26 (100)**
Scap	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**36 (100)**	0 (0.0)	36 (100)	**36 (100)**
Hum	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.1)**	0 (0.0)	1 (2.1)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (4.2)**	0 (0.0)	2 (4.2)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**48 (100)**	0 (0.0)	48 (100)	**51 (106)**
Rad	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**26 (100)**	0 (0.0)	26 (100)	**26 (100)**
Uln	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (4.8)**	0 (0.0)	1 (4.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**21 (100)**	0 (0.0)	21 (100)	**22 (105)**
Mtc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**111 (100**	0 (0.0)	111 (100)	**111 (100)**
Pel	**1 (2.0)**	0 (0.0)	1 (2.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**4 (7.8)**	0 (0.0)	4 (7.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**51 (100)**	0 (0.0)	51 (100)	**56 (110)**
Fem	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (3.8)**	0 (0.0)	2 (3.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**52 (100)**	0 (0.0)	52 (100)	**54 (104)**
Pat	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**17 (100)**	0 (0.0)	17 (100)	**17 (100)**
Tib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.7)**	0 (0.0)	1 (2.7)	**5 (13.5)**	0 (0.0)	5 (13.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (2.7)**	0 (0.0)	1 (2.7)	**37 (100)**	0 (0.0)	37 (100)	**44 (119)**
Fib	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**11 (100)**	0 (0.0)	11 (100)	**11 (100)**
Calc	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**16 (80.0)**	0 (0.0)	16 (80.0)	**16 (80.0)**
Ast	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**15 (78.9)**	0 (0.0)	15 (78.9)	**15 (78.9)**
Mtt	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.3)**	0 (0.0)	1 (1.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (1.3)**	0 (0.0)	1 (1.5)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**67 (84.8)**	0 (0.0)	67 (84.8)	**69 (87.3)**
Carp/tars	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**81 (83.5)**	0 (0.0)	81 (83.5)	**81 (83.5)**
Phlx 1/2	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**2 (0.6)**	0 (0.0)	2 (0.7)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**287 (92.3**	0 (0.0)	287 (92.3	**21 (6.8)**
Phlx 3	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**138 (92.0**	0 (0.0)	138 (92.0	**5 (3.3)**
NISP Total	**2 (0.1)**	0 (0.0)	2 (0.1)	**5 (0.3)**	0 (0.0)	5 (0.3)	**8 (0.4)**	0 (0.0)	8 (0.5)	**22 (1.2)**	0 (0.0)	22 (1.3)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (0.1)**	0 (0.0)	1 (0.1)	**1709 (96.**	0 (0.0)	1709 (96.	**1346 (75.6**
Vert indet	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**58 (100)**	0 (0.0)	58 (100)	**58 (100)**
LBS	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**27 (100)**	0 (0.0)	27 (100)	**27 (100)**
FRG>2mm	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**788 (100**	0 (0.0)	788 (100)	**788 (100)**
Tooth frag	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**0 (0.0)**	0 (0.0)	0 (0.0)	**29 (100)**	0 (0.0)	29 (100)	**29 (100)**
N Total	**2 (0.1)**	0 (0.0)	2 (0.1)	**5 (0.2)**	0 (0.0)	5 (0.2)	**8 (0.3)**	0 (0.0)	8 (0.3)	**22 (0.8)**	0 (0.0)	22 (0.8)	**0 (0.0)**	0 (0.0)	0 (0.0)	**1 (0.0)**	0 (0.0)	1 (0.0)	**2611 (97.**	0 (0.0)	2611 (97.	**2649 (98.7**

APPENDIX H

Skeletal-part representation, fragmentation, digestion, and beak/tooth puncture comparisons between small mammal remains from ingested (pellets & scats) and non-ingested (surface & nest) diurnal and nocturnal raptors and carnivores.

n/r = not reported
"A. Fragmentation" based on all reported NISP and MNE values.
"B. Fragmentation" based on the most commonly reported NISP and MNE values: maxilla, mandible, scapula, humerus, radius, ulna, pelvis, femur, and tibia.
1. Armstrong & Avery; 2. Cruz-Uribe & Klein, 1998; 3. McGraw et al., 2006; 4. Sanders et al., 2003; 5. Trapani et al., 2006; 6. Lloveras et al., 2008a; 7. Hockett, 1991; 8. Hockett, 1995; 9. Sanchis Serra, 2000; 10. Lloveras et al., 2009; 11. Cochard, 2004; 12. Hockett & Haws, 2002; 13. Hockett, 1999; 14. Lloveras et al., 2008b; 15. Rodríguez-Hidalgo et al., 2013b; 16. Schmitt & Juell, 1994
* Beak/teeth marks total include all reported beak or tooth derived marks reported by the authors. These include: punctures, pits, notches, scores, and gnawing and exclude digestion. These marks have been summed due to the multiple ways in which they are reported in the literature.

Predator	**Diurnal raptors** Verreaux's Eagle *(Aquila verreauxii)*												
Origin	Pellets	Pellets	Pellets	Pellets	Surface	Surface	Surface	Surface	Surface	Surface	**Pellet & surface**	Surface	Surface
Prey	Leporid[1] %RA	Hyrax[1] %RA	Mole-rat[1] %RA	Total[1] %RA	Leporid[1] %RA	Hyrax[1] %RA	Mole-rat[1] %RA	Carn.[1] %RA	Bovid[1] %RA	Total[1] %RA	**Total[1] %RA**	Hyrax[2] %MNI	Leporid[2] %MNI
Maxilla (Crania)	0.50	0.50	0.50	0.50	0.14	0.91	0.97	0.79	0.11	0.81	**0.82**	1.00	0.23
Mandible	0.00	0.00	0.00	0.00	0.03	0.97	0.52	0.36	0.46	0.70	**0.70**	0.81	0.10
Teeth	0.00	0.06	0.00	0.02	0.01	0.01	0.01	0.01	0.00	0.01	**0.01**	-	-
Atlas	0.00	1.00	0.00	0.33	0.00	0.02	0.00	0.00	0.07	0.01	**0.01**	0.00	0.00
Axis	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	**0.00**	0.00	0.00
Cervicals	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.01	0.01	**0.01**	0.00	0.00
Thoracics	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.01	**0.01**	0.00	0.10
Lumbars	0.00	0.14	0.00	0.05	0.34	0.03	0.01	0.00	0.00	0.05	**0.05**	0.00	0.45
Caudal	0.00	0.40	0.00	0.06	0.00	0.01	0.00	0.00	0.00	0.00	**0.00**	-	-
Vertebrae total	0.00	0.13	0.00	0.05	0.11	0.01	0.00	0.00	0.07	0.02	**0.02**	0.00	0.45
Sacrum	0.00	0.00	0.00	0.00	0.56	0.02	0.03	0.00	0.00	0.07	**0.07**	0.02	0.62
Ribs	0.00	0.00	0.03	0.01	0.01	0.00	0.00	0.00	0.01	0.00	**0.00**	0.01	0.00
Scapula	0.00	0.00	0.00	0.00	0.01	0.07	0.01	0.00	0.04	0.04	**0.04**	0.04	0.16
Humerus	0.00	0.00	0.00	0.00	0.14	0.07	0.09	0.14	0.18	0.09	**0.09**	0.06	0.25
Radius	0.00	0.00	0.50	0.17	0.17	0.02	0.01	0.04	0.07	0.03	**0.03**	0.01	0.12
Ulna	0.00	0.00	0.50	0.17	0.13	0.01	0.07	0.07	0.07	0.04	**0.05**	0.02	0.07
Metacarp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	**0.00**	-	-
Pelvis	0.00	0.00	0.00	0.00	0.82	0.42	0.16	0.07	0.18	0.36	**0.36**	0.19	1.00
Femur	0.00	0.00	0.00	0.00	0.36	0.08	0.12	0.11	0.29	0.13	**0.13**	0.10	0.55
Patella	0.00	0.00	0.50	0.17	0.01	0.01	0.00	0.00	0.04	0.01	**0.01**	0.01	0.00
Tibia	0.00	0.00	0.00	0.00	0.74	0.04	0.17	0.11	0.29	0.15	**0.16**	0.05	0.95
Fibula	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.04	0.07	0.02	**0.01**	0.00	-
Calcan	0.00	0.00	0.00	0.00	0.22	0.02	0.03	0.07	0.07	0.05	**0.05**	0.00	0.45
Astrag	0.00	0.00	0.00	0.00	0.21	0.03	0.01	0.00	0.07	0.04	**0.04**	0.00	0.30
Carpals/tarsals	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**	-	-
Metatars	0.00	0.00	0.00	0.00	0.16	0.01	0.01	0.00	0.11	0.02	**0.02**	-	-
Phal 1/2	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.02	0.01	**0.01**	-	-
Phal 3	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.01	**0.01**	-	-
Phal total	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.01	0.01	**0.01**	-	-
Metapodial tot.	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.13	0.01	**0.01**	-	-
NISP total	2	7	5	14	593	1490	705	54	104	2946	**2960**	n/r	n/r
MNE total	1	7	5	13	480	1240	538	52	71	2381	**2394**	n/r	n/r
MNI	1	1	1	3	36	192	107	14	14	363	**366**	3487	31
A. Fragmentation (NISP/MNE)	2.00	1.00	1.00	1.08	1.24	1.20	1.31	1.04	1.46	1.24	**1.23**	n/r	n/r
B. Fragmentation (NISP/MNE)	2.00	1.00	1.00	1.20	1.51	1.23	1.34	1.04	1.64	1.27	**1.30**	n/r	n/r
% Complete long bones	-	-	0.0	0.0	60.5	45.5	70.4	78.6	62.5	63.7	**63.5**	n/r	n/r
% Complete all bones	0.0	57.1	20.0	35.7	63.9	52.4	47.7	79.2	53.5	51.8	**54.1**	n/r	n/r
% Beak/teeth punctures	0.0	0.0	0.0	0.0	4.6	10.5	10.1	15.0	13.0	9.0	**9.3**	n/r	n/r
% Beak/teeth marks total*	0.0	0.0	0.0	0.0	7.3	13.1	13.8	19.0	18.3	10.4	**12.3**	n/r	n/r
% Digested	100.0	100.0	100.0	100.0	0.2	0.0	0.0	0.0	0.0	0.2	**0.6**	n/r	n/r

Bald Eagle (*Haliaeetus leucocephalus*)						Martial Eagle (*Polemaetus bellicosus*)		African Crowned Eagle (*Stephanoaetus coronatus*)				Spanish Imperial Eagle (*Aquila adalberti*)	Northern Harrier (*Circus cyaneus*)	Golden Eagle (*Aquila chrysaetos*)	Prairie Falcon (*Falco mexicanus*)
Pellets	Surface	Pellet & surface	Pellets	Surface	Pellet & surface	Surface	Surface	Surface	Surface	Surface	Surface	Pellets	Pellets	Surface	Surface
Leporid %RA	Leporid %RA	Leporid %RA	Guinea Pig %RA	Guinea Pig %RA	Guinea Pig %RA	Hyrax[2] %MNI	Leporid[2] %MNI	Hyrax[2] %MNI	Primate[3] %RA	Primate[4] %RA	Redtail[5] %RA	Leporid[6] %RA	Leporid[7] %MAU	Leporid[8] %MAU	Leporid[8] %MAU
0.05	0.95	1.00	0.60	0.40	1.00	0.98	0.00	1.00	0.26	0.49	0.55	0.44	0.00	0.06	0.19
0.00	1.00	1.00	0.55	0.45	1.00	1.00	0.00	0.81	0.1	0.1	0.1	0.34	1.00	0.00	0.42
0.05	0.93	0.98	0.28	0.47	0.75	-	-	-	-	-	-	0.43	0.00	0.00	-
0.00	0.90	0.90	0.10	0.80	0.90	0.00	0.00	0.00	-	-	-	-	-	-	-
0.00	0.90	0.90	0.10	0.50	0.60	0.00	0.00	0.00	-	-	-	-	-	-	-
0.40	0.56	0.96	0.30	0.18	0.48	0.00	0.01	0.00	-	-	-	-	-	-	-
0.01	0.90	0.91	0.21	0.28	0.49	0.00	0.03	0.00	-	-	-	-	-	-	-
0.00	0.97	0.97	0.25	0.45	0.70	0.00	0.38	0.00	-	-	-	-	-	-	-
0.14	0.51	0.65	0.30	0.10	0.40	-	-	-	-	-	-	-	-	-	-
0.09	0.79	0.88	0.21	0.39	0.60	0.00	0.38	0.00	0.02	0.0	0.04	0.06	0.00	-	-
0.00	0.88	0.88	0.05	0.80	0.85	0.00	0.55	0.00	0.05	0.0	0.03	-	0.00	0.47	0.38
0.06	0.60	0.66	0.10	0.19	0.29	0.00	0.00	0.00	0.01	0.0	0.01	0.02	-	-	-
0.20	0.80	1.00	0.35	0.55	0.90	0.00	0.01	0.12	0.1	0.2	0.14	0.16	0.85	0.06	0.08
0.15	0.85	1.00	0.30	0.50	0.80	0.10	0.04	0.04	0.15	0.1	0.06	0.16	1.00	0.09	0.54
0.10	0.85	0.95	0.30	0.55	0.85	0.05	0.04	0.00	0.08	0.1	0.05	0.03	0.85	0.18	0.38
0.15	0.85	1.00	0.40	0.55	0.95	0.11	0.06	0.00	0.125	0.0	0.05	0.25	1.00	0.18	0.38
0.05	0.95	1.00	0.39	0.60	0.99	-	-	-	-	-	-	0.04	0.00	-	-
0.00	1.00	1.00	0.15	0.85	1.00	0.60	1.00	0.22	0.06	0.1	0.07	0.06	0.08	0.26	0.46
0.00	1.00	1.00	0.15	0.85	1.00	0.40	0.60	0.03	0.25	0.4	0.28	0.03	0.08	0.44	0.42
0.00	0.80	0.80	0.00	0.80	0.80	0.04	0.00	0.00	-	0.0	0.02	0.22	-	-	-
0.00	1.00	1.00	0.15	0.85	1.00	0.32	0.95	0.05	0.2	0.25	0.21	0.50	0.08	0.94	1.00
-	-	-	0.00	0.85	0.85	0.00	-	0.00	0.15	0.2	0.2	-	-	-	-
0.00	1.00	1.00	0.10	0.90	1.00	0.03	0.43	0.00	-	0.1	0.1	0.41	0.00	1.00	0.69
0.00	1.00	1.00	0.05	0.90	0.95	0.03	0.41	0.00	-	0.0	0.0	0.19	0.00	0.97	0.65
0.05	0.93	0.98	0.15	0.70	0.85	-	-	-	-	0.0	0.0	0.05	-	-	-
0.00	1.00	1.00	0.08	0.90	0.98	-	-	-	-	-	-	0.15	0.00	-	-
0.05	0.95	1.00	0.24	0.66	0.90	-	-	-	-	-	-	0.17	0.00	-	-
0.03	0.94	0.97	0.16	0.66	0.82	-	-	-	-	-	-	0.99	0.00	-	-
0.04	0.95	0.99	0.20	0.66	0.86	-	-	-	-	0.0	0.0	0.46	0.00	-	-
0.03	0.97	1.00	0.24	0.75	0.99	-	-	-	0.01	0.0	0.0	0.09	0.00	-	-
157	1992	2149	483	987	1470	n/r	n/r	n/r	669	413	559	824	65	156	165
109	1883	1992	372	933	1305	n/r	n/r	n/r	n/r	n/r	545	737	64	150	141
2	10	10	6	9	10	70	75	678	204	68	103	16	n/r	n/r	n/r
1.35	1.06	1.08	1.30	1.06	1.13	n/r	n/r	n/r	n/r	n/r	1.03	1.12	1.02	1.04	1.17
2.00	1.31	1.39	0.00	1.30	1.44	n/r	n/r	n/r	n/r	n/r	n/r	1.66	1.02	1.08	1.24
0.0	92.3	70.6	0.0	69.6	41.2	n/r	n/r	n/r	61.0	n/r	58.0	0.0	72.5	n/r	n/r
47.1	76.8	74.6	24.0	78.4	61.7	n/r	n/r	n/r	41.0	n/r	61.0	27.9	n/r	n/r	n/r
0.3	0.3	0.3	0.4	1.1	0.8	n/r	n/r	n/r	n/r	n/r	n/r	n/r	n/r	1.0-2.0	1.0-2.0
0.3	1.5	1.4	0.4	2.1	1.6	n/r	n/r	n/r	n/r	n/r	n/r	n/r	n/r	n/r	n/r
100.0	0.0	7.2	100.0	0.0	32.9	n/r	n/r	n/r	n/r	n/r	n/r	98.0	n/r	n/r	n/r

Nocturnal raptors											
Eurasian Eagle-Owl *(Bubo bubo)*			Barn Owl *(Tyto*	Great Horned Owl *(Bubo virginianus)*						
Pellets & surface Leporid[9] %MNI	Pellets & surface Leporid[10] %RA	Pellets & surface Leporid[10] %RA	Pellets Leporid[8] %MAU	Pellets Leporid[8] %MAU	Pellets Leporid %RA	Surface Leporid %RA	**Pellet & surface Leporid %RA**	Pellets Guinea Pig %RA	Surface Guinea Pig %RA	**Pellet & surface Guinea Pig %RA**
0.28	0.47	0.31	0.66	0.41	0.50	0.50	**1.00**	0.20	0.80	**1.00**
0.32	0.24	0.42	0.83	0.55	0.60	0.40	**1.00**	0.40	0.60	**1.00**
-	0.21	0.27	-	-	0.45	0.42	**0.87**	0.32	0.58	**0.90**
-	-	-	-	-	0.60	0.30	**0.90**	0.40	0.50	**0.90**
-	-	-	-	-	0.70	0.30	**1.00**	0.50	0.40	**0.90**
0.05	-	-	-	-	0.76	0.20	**0.96**	0.74	0.18	**0.92**
0.20	-	-	-	-	0.64	0.18	**0.82**	0.75	0.16	**0.91**
0.45	-	-	-	-	0.21	0.74	**0.95**	0.47	0.43	**0.90**
-	-	-	-	-	0.26	0.53	**0.79**	0.24	0.48	**0.72**
0.23	0.35	0.22	-	-	0.53	0.38	**0.91**	0.52	0.36	**0.88**
0.47	-	-	0.26	0.50	0.00	0.83	**0.83**	0.50	0.45	**0.95**
-	0.29	0.36	-	-	0.50	0.18	**0.68**	0.48	0.22	**0.70**
0.29	0.16	0.12	0.57	0.59	0.30	0.70	**1.00**	0.65	0.30	**0.95**
0.54	0.34	0.23	1.00	0.66	0.35	0.65	**1.00**	0.65	0.35	**1.00**
0.35	0.32	0.10	0.43	1.00	0.35	0.65	**1.00**	0.50	0.35	**0.85**
0.46	0.24	0.23	0.88	0.73	0.35	0.65	**1.00**	0.60	0.35	**0.95**
0.14	0.14	0.14	-	-	0.34	0.65	**0.99**	0.63	0.35	**0.98**
0.75	0.90	0.63	0.46	0.82	0.05	0.95	**1.00**	0.10	0.90	**1.00**
0.81	0.90	0.54	0.56	0.50	0.10	0.90	**1.00**	0.25	0.75	**1.00**
-	0.95	0.62	-	-	0.00	0.85	**0.85**	0.35	0.50	**0.85**
0.56	0.68	0.63	0.51	0.48	0.10	0.90	**1.00**	0.40	0.60	**1.00**
-	-	-	-	-	-	-	**-**	0.30	0.55	**0.85**
0.37	0.92	0.92	0.92	0.52	0.25	0.75	**1.00**	0.40	0.60	**1.00**
0.22	0.71	0.56	0.40	0.27	0.25	0.75	**1.00**	0.40	0.60	**1.00**
-	0.18	0.11	-	-	0.19	0.73	**0.92**	0.30	0.55	**0.85**
0.44	0.71	0.63	-	-	0.18	0.80	**0.98**	0.40	0.60	**1.00**
-	0.47	0.25	-	-	0.26	0.72	**0.98**	0.51	0.45	**0.96**
-	0.37	0.14	-	-	0.24	0.72	**0.96**	0.46	0.46	**0.92**
-	0.41	0.21	-	-	0.25	0.72	**0.97**	0.49	0.46	**0.95**
-	0.37	0.36	-	-	0.26	0.73	**0.99**	0.52	0.48	**1.00**
6454	1794	1926	1639	418	1444	1285	**2729**	1274	805	**2079**
n/r	1269	1370	1146	298	751	1225	**1976**	857	769	**1626**
222	19	26	n/r	n/r	2	10	**10**	6	9	**10**
n/r	1.41	1.41	1.43	1.40	1.92	1.05	**1.38**	1.49	1.05	**1.28**
n/r	2.22	2.87	1.54	1.48	4.89	1.34	**2.40**	2.96	1.26	**1.90**
48.0	14.6	10.8	n/r	n/r	0.0	98.7	**75.2**	1.9	83.1	**63.6**
49.5	53.9	45.9	n/r	n/r	24.1	85.6	**53.1**	30.5	78.5	**48.4**
present	2.0	1.3	1.4	1.0	1.0	1.0	**0.8**	0.5	0.5	**0.5**
present	n/r	n/r	n/r	n/r	1.8	4.1	**2.9**	0.9	1.5	**1.1**
~50.0	68.8	65.6	n/r	n/r	100.0	0.0	**52.9**	100.0	0.0	**61.3**

Carnivores															
Red Fox		Red Fox		Red Fox &/or Iberian Lynx (Vulpes vulpes)		Iberian lynx		Coyote							
(Vulpes vulpes)		*(Vulpes vulpes)*		*(Lynx pardinus)*		*(Lynx pardinus)*		*(Canis latrans)*							
Scat & surface	Surface	Surface	Scat	Surface	Surface	Scat	Surface	Scat	Scat	Surface	**Scat & Surface**	Scat	Surface	**Scat & Surface**
Leporid[9] %MNI	Leporid[11] %RA	Leporid[17] %RA	Leporid[17] %RA	Leporid[12] ?%RA?	Leporid[13] %RA	Leporid[14] %RA	Leporid[15] %RA	Leporids[16] ?%MAU?	Leporids %RA	Leporids %RA	**Leporids %RA**	Guinea Pig %RA	Guinea Pig %RA	**Guinea Pig %RA**
-	0.08	0	0.25	0.56	0.29	0.64	0.51	-	0.85	0.10	**0.95**	0.70	0.00	**0.70**
-	0.50	0.91	0.25	0.39	0.48	0.82	0.41	1.00	0.85	0.10	**0.95**	0.75	0.00	**0.75**
-	0.25	0.07	0.21	-	-	0.77	0.36	-	0.60	0.08	**0.68**	0.64	0.00	**0.64**
-	0.05	-	-	-	-	-	-	-	0.70	0.00	**0.70**	0.60	0.00	**0.60**
-	0.00	-	-	-	-	-	-	-	0.80	0.00	**0.80**	0.80	0.00	**0.80**
-	0.05	-	-	-	-	-	-	-	0.54	0.00	**0.54**	0.28	0.00	**0.28**
-	0.00	-	-	-	-	-	-	-	0.20	0.00	**0.20**	0.21	0.00	**0.21**
-	0.13	-	-	-	-	-	-	-	0.14	0.00	**0.14**	0.32	0.00	**0.32**
-	0.00	-	-	-	-	-	-	-	0.42	0.00	**0.42**	0.70	0.00	**0.70**
-	0.05	0.06	0.17	2.9	0.22	0.17	0.17	-	0.47	0.00	**0.47**	0.46	0.00	**0.46**
-	0.16	-	-	0.11	0.19	-	-	-	0.25	0.00	**0.25**	0.49	0.00	**0.49**
-	0.05	0	0.15	-	0.04	0.18	0.16	-	0.47	0.00	**0.47**	0.07	0.00	**0.07**
-	0.29	0	0.75	0.11	0.19	0.54	0.08	0.40	0.85	0.00	**0.85**	0.70	0.00	**0.70**
-	0.53	0.05	0.75	0.28	0.33	0.57	0.22	0.37	0.80	0.00	**0.80**	0.80	0.00	**0.80**
-	0.32	0.27	0.75	0	0.25	0.43	0.75	0.37	0.80	0.10	**0.90**	0.65	0.00	**0.65**
-	0.63	0.27	0.50	0.17	0.31	0.61	0.66	0.50	0.80	0.10	**0.90**	0.70	0.00	**0.70**
-	0.47	0.22	0.00	-	-	0.41	0.52	-	0.57	0.25	**0.82**	0.95	0.00	**0.95**
-	0.95	0	0.00	1	0.73	0.61	0.90	0.33	0.80	0.00	**0.80**	0.60	0.00	**0.60**
-	0.42	0	0.50	0.67	0.67	0.64	0.36	0.63	0.90	0.00	**0.90**	0.80	0.00	**0.80**
-	0.00	0	0.00	-	0.04	0.43	0.01	-	0.85	0.00	**0.85**	0.80	0.00	**0.80**
-	0.63	0.73	0.25	0.89	1.00	0.43	1.00	0.23	0.55	0.30	**0.85**	0.70	0.00	**0.70**
-	-	-	-	-	-	-	-	-	-	-	**-**	0.25	0.00	**0.25**
-	0.53	0.73	0.25	-	0.60	0.39	1.00	-	0.55	0.30	**0.85**	0.70	0.20	**0.90**
-	0.47	0.77	0.00	-	0.27	0.25	0.91	-	0.60	0.30	**0.90**	0.70	0.20	**0.90**
-	0.11	0.38	0.08	-	0.69	0.16	0.45	-	0.41	0.26	**0.67**	0.45	0.09	**0.54**
-	0.55	0.9	0.25	-	-	0.27	0.90	-	0.58	0.30	**0.88**	0.80	0.20	**1.00**
-	0.15	0.56	0.24	-	-	0.37	-	-	0.62	0.27	**0.89**	0.89	0.09	**0.98**
-	0.04	0.53	0.08	-	-	0.58	-	-	0.64	0.25	**0.89**	0.90	0.09	**0.99**
-	0.11	-	-	-	0.10	0.42	0.46	-	0.63	0.26	**0.89**	0.90	0.09	**0.99**
-	0.38	-	-	-	0.20	0.35	0.69	-	0.58	0.28	**0.86**	0.88	0.10	**0.98**
10009	743	639	113	76	739	1515	8772	840	2138	332	**2470**	1709	72	**1781**
n/r	632	620	76	72	726	1105	8567	480	1166	303	**1469**	1041	72	**1113**
15	19	11	2	n/r	26	14	107	n/r	9	3	**10**	10	2	**10**
n/r	1.18	1.03	1.49	1.06	1.02	1.37	1.02	1.75	1.83	1.10	**1.68**	1.64	1.00	**1.60**
n/r	1.42	1.26	2.00	n/r	1.06	2.22	1.17	n/r	4.18	2.29	**4.01**	3.33	-	**3.33**
18.6	45.4	5.4	0.0	n/r	n/r	2.5	39.4	0	0.0	0.0	**0.0**	1.3	-	**0.5**
36.9	65.0	89.4	12.0	n/r	n/r	43.0	77.8	7.1	25.1	87.3	**33.5**	42.1	100.0	**44.5**
present	6.5	n/r	n/r	24.0	8.8	0.3	0.9	0.1	1.0	0.3	**0.9**	0.1	0.0	**0.1**
n/r	19.9	9.5	3.0	n/r	n/r	n/r	n/r	n/r	1.8	0.3	**1.6**	0.5	0.0	**0.4**
>50.0	12.4	0	99.5	n/r	n/r	97.2	0	100.0	100.0	0.0	**86.6**	100.0	0.0	**96.0**